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CONTENTS

PAGE

Brian, M. V., and Brian, A. D. Observations on the taxonomy of the ants *Myrmica rubra* L. and *M. laevinodis* Nylander (Hymenoptera: Formicidae) . . . 393

Butler, P. M., M.A., Ph.D. Observations on the biology of *Palorus ratzeburgi* Wissman, with comparative notes on Tenebrionidae in general (Coleoptera) . . 249

Cumber, R. A., B.Sc.(N.Z.), Ph.D., D.I.C., F.R.E.S. The biology of Humble-Bees, with special reference to the production of the worker caste 1

Dirsh, V. M., D.Sc. The genus *Thalpomena* Saussure, 1884 (Orthoptera, Acrididae) and its allies 363

Fraser, Lt.-Col. F. C., I.M.S. (Retd.), F.R.E.S. The Zygoptera of Mauritius (Order Odonata) 135

Gillies, M. T., B.A., M.B., B.Ch. Notes on some Ephemeroptera Baëtidae from India and South-East Asia 161

Hale Carpenter, Emeritus Professor G. D., M.B.E., D.M. *Pseudacraea eurytus* (L.) (Lep. Nymphalidae): A study of a polymorphic mimic in various degrees of speciation 71

Hickin, N. E., Ph.D. Pupae of the British Trichoptera 275

Khalifa, A., B.Sc.(Cairo), Ph.D.(Cantab.). Spermatophore production in Trichoptera and some other insects 449

Pagden, H. T., M.A., F.R.E.S. Descriptions and records of Austro-Malaysian Methocidae and Mutillidae (Hymenoptera) 191

Parker, Alec H. Observations on the seasonal and daily incidence of certain biting midges (*Culicoides* Latreille—Diptera, Ceratopogonidae) in Scotland . . 179

Phipps, John, M.Sc., D.I.C., F.R.E.S. The structure and maturation of the ovaries in British Acrididae (Orthoptera) 233

Roepke, W., Ph.D. The genus *Nyctemera* Hübner 47

Satchell, G. H., B.Sc., Ph.D. The early stages of the British species of *Pericoma* Walker. (Diptera: Psychodidae.) 411

Tottenham, The Rev. C. E., M.A., F.R.E.S. Studies in the genus *Philonthus* Stephens (Coleoptera) 291

Waloff, N., Ph.D., F.R.E.S. Observations on larvae of *Ephestia elutella* Hübner (Lep. Phycitidae) during diapause 147

3 p.c

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CONTENTS

PAGE

Cumber, R. A., B.Sc.(N.Z.), Ph.D., D.I.C., F.R.E.S. The Biology of Humble-Bees, with special reference to the production of the Worker Caste . . . . 1–45, 10 figs.

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THE BIOLOGY OF HUMBLE-BEES, WITH SPECIAL REFERENCE TO THE PRODUCTION OF THE WORKER CASTE.

By R. A. Cumber, B.Sc.(N.Z.), Ph.D., D.I.C., F.R.E.S.

Manuscript received 9th February, 1948.

(Read 2nd June, 1948.)

With 10 Text-figures.

Contents.

	PAGE
1. Introduction and acknowledgments	1
2. Some features from the general biology which have a bearing on the problems considered	2
(*a*) The ovarial development of spring queens	2
(*b*) Temperatures in nests	2
(*c*) Larval nutrition	2
(*d*) Parasites	3
3. The production of the worker caste. Population changes and organization	4
(*a*) Mechanism of production and definition of worker caste in Bombidae	4
(*b*) Method of nutrition: its effect on the size of adult individuals	6
(*c*) The seasonal variation in size of female individuals	7
(*d*) A division of labour	16
(*e*) The development of ovaries in workers	19
4. The production of queens	22
(*a*) Differences between queen and worker	22
(*b*) The differentiation of queen and worker on a biometric basis	24
(*c*) Brood data in nests producing queens	29
(*d*) Possible factors in queen production	33
5. Discussion	40
6. Summary	43
7. Bibliography	44

1. Introduction and Acknowledgments.

The study of humble-bees in Buckinghamshire, Berkshire and Surrey during 1946 and 1947 has provided information relating to the problems of worker and queen production and population changes and organization.[1] Statistical evidence on new and previously described phenomena are presented.

The work has been carried out at the Imperial College of Science and Technology, and I wish to express my thanks to the staff of the Department of Zoology and Applied Entomology, especially to Dr. O. W. Richards, for advice throughout the course of the work. I wish also to thank Dr. G. Salt, of the Zoology Department, Cambridge, for his many helpful suggestions.

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[1] A manuscript of the detailed observations which are summarized in this paper will be deposited in the library of the Royal Entomological Society.

2. SOME FEATURES FROM THE GENERAL BIOLOGY WHICH HAVE A BEARING ON THE PROBLEMS CONSIDERED.

(a) *The Ovarial Development of " Spring " Queens.*

Those queens which have successfully hibernated are called for convenience " spring " queens in contrast to the " autumn " queens, which are those produced at the climax of colonial development.

When the " spring " queens emerge from hibernation their ovaries show no development, and resemble those of the " autumn " queens. When they have been feeding for about three weeks, during which time they have increased noticeably in weight (Table I), the ovarioles begin to swell until the rudiments of the ova may be seen between the growing groups of nurse cells. At this stage the queens begin searching for nesting sites. A little later they begin to gather pollen, and dissection at this stage shows the presence of several well developed eggs.

It is thus apparent that whereas in workers the development of ovaries may occur without great delay, the ovaries of queens do not develop till after a hibernation period, followed by a period of active feeding.

Table I shows the increase in weight of unparasitized " spring " queens of *Bombus lucorum* (L.) taken at Putney Heath, Surrey, in 1947.

TABLE I.—*Weight Increase in " Spring " Queens of* B. lucorum.

Date.	Number of specimens.	Average weight (mg.).	Weight range (mg.).
11.iv.47	3	384·3	339–430
15.iv.47	13	446·2	368–534
16.iv.47	11	428·7	380–499
24.iv.47	14	444·8	315–511
29.iv–7.v.47	6	493·0	401–609

(b) *Temperatures in Nests.*

The work of Lindhard (1912), Himmer (1933), and Nielsen (1938), has provided data on nest temperatures. During the present work, temperature records have been kept for both underground and surface-nesting species.

In the incipient stages both types of nest are very susceptible to changes in external temperatures, but in surface nests there is in addition the effect of direct sunlight and wind. In the early stages of all nests temperatures tend to fluctuate between 20 and 25 deg. C., and are several degrees above external temperatures. As nests become more populous and the amount of brood increases, higher and more stable (especially in underground nests) temperatures are maintained. At the climax of colonial development when sexual brood is present, temperatures of between 30 and 34 deg. C. are recorded.

Doubtless these higher temperatures provide optimum conditions for the work and growth of the colony, and are accompanying factors of a developmental state and necessary for queen production.

(c) *Larval Nutrition.*

Differences in methods of nutrition during the life of the individual larva seem to be for the most part specific rather than associated with the development of the type of individual.

In some species egg-chambers are always "primed" with bee-bread, whereas in others only the initial egg group of the queen is "primed."

Two methods of larval nutrition subsequent to those in the initial egg-chamber were recognized by Sladen in 1898, when he divided English species into "pouch-makers" (changed to "pocket-makers" 1912) and "pollen-storers."

In the "pocket-makers" an opening is made in the wax beneath or at the side of the larval group, and this is plugged with bee-bread. As the larval group grows, and the wax above is spread to accommodate the growing "morula," we find the larvae eventually resting on or alongside a bed of bee-bread, on which they are observed to feed. In addition to this store of food, workers break the wax and feed the larvae with a regurgitated mixture of pollen and honey. According to Plath (1934), this "pocket-making" habit is lost in some species amongst the later brood (male and queen), which are fed purely by regurgitation. In *Bombus agrorum* (F.) the "pocket-making" habit persists for all broods.

In the "pollen-storers" the larvae are in the equivalent stages, fed only by rupture of the wax envelope and the addition of food materials in the form of a regurgitated mixture which contains pollen and honey.

As will be shown later, this division of Sladen's is a very important one.

(d) *Parasites.*

Parasites affect both the individual and the colony as a whole, and both brood and adult parasites are common. Nests which are heavily parasitized may not develop normally, and this fact has to be taken into account when considering the life of the colony.

Several writers have been puzzled by the appearance in summer of searching queens which should have founded colonies much earlier. The dissection of these almost invariably shows that they are old individuals parasitized by the Nematode worm *Sphaerularia bombi* Duf., and not queens of the new generation.

Perhaps the most important parasite to be considered is the Tachinid fly *Brachycoma devia* (Fall.), which is responsible for a very heavy toll amongst humble-bee populations, and is probably mainly responsible for the premature death of many colonies. Such heavily infected colonies cannot be considered as normal. But even in large and prosperous queen-producing colonies this parasite may account for over 100 pupae. It is usual for nests to have some degree of parasitization, but heavy infection must undoubtedly have its effect on brood/worker ratios, etc.

Conopid parasites have provided evidence of a foraging caste. Adult Conopid flies lay their eggs in the abdomens of foraging workers, where the larvae grow and consume the contents, ultimately pupating *in situ*. On fine sunny days when the nest is active, if samples of "nurse" bees and "foragers" are dissected, it will often be found that numbers of "foragers" are parasitized, and there is no infection of the "nurse" bees.

The parasitic humble-bee, *Psithyrus*, is of considerable interest in connection with the problem of caste production, for no workers are produced. Small female individuals of some species of this parasite are occasionally found, however. It is assumed that the parasitic brood is only produced under certain conditions in the nest. It may well be that in most cases the development of the ovaries of the *Psithyrus* queen is dependent upon a certain state of economy in the nest, and that subsequent brood is produced at reduced brood/worker ratios.

3. THE PRODUCTION OF THE WORKER CASTE. POPULATION CHANGES AND ORGANIZATION.

(a) *Mechanism of Production and Definition of the Worker Caste in* BOMBIDAE.

No definite evidence has been found to alter the existing belief that the production of the worker caste is due to quantitative feeding in the larval stages. This condition has been described by Wheeler (1922), who writes as follows: "Owing to the number of larvae which are reared simultaneously, especially during the earlier stages of colony formation, they are inadequately nourished and have to pupate as rather small individuals, with poorly developed ovaries. Such individuals therefore become workers. This inhibition of ovarial development, which has been called "alimentary castration," is maintained during the adult life of most workers by the exigencies of the nursing instincts. The workers have to complete and care for the nest, forage for food, and distribute most of it among their larval sisters. All this exhausting labour on slender rations tends to keep them sterile. In other words "nutricial castration" (derived from nutrix, a nurse), to use Marchal's terms, takes the place in the adult worker of alimentary castration, to which it was subjected during its larval period. It is only later in the development of the colony, when the number of workers and consequently also the amount of food brought in have considerably increased, and the labour of foraging and nest construction have correspondingly decreased for the individual worker, that the larvae can be more copiously fed and develop as fertile females or queens. At that season, too, some of the workers may develop their ovaries, but as the members of the worker caste are incapable of fecundation, they can lay only male-producing eggs. This . . . may suffice to explain the conditions in the social wasps and social bees."

Frison (1927) expresses the same idea as follows: ". . . the increase in size of workers is correlated with conditions which suggest that the amount or quality of food is the factor which determines whether a female egg will produce small workers, large workers, or queens."

The most conclusive evidence supporting this belief is seen in the following experiment described by Sladen in 1912. "Development of Queen: I have succeeded in getting queens reared by *B. latreillellus* from eggs laid early in the queen's life in the following manner: Two *latreillellus* nests, in which a few workers had already emerged from the first batch of cocoons, were joined together, and the queens and all the young larvae were removed, and also all the eggs except three. The larvae that hatched from these three eggs had thus about twenty workers to care for them exclusively, and they developed into females as large as queens. That they were really queens and not giant workers was shown by the fact that they paid no attention to the brood that was subsequently reared, and as soon as they were old enough to fly they left the nest for good."

A more recent theory of caste differentiation indicated as possibly applying in the BOMBIDAE has been put forward by Flanders (1942, '45, '46). This is based on the phenomenon of oösorption which is known to occur in some parasitic Hymenoptera.

Flanders (1945) advanced the hypothesis that the " rate of egg deposition (in so far as it affects the nutrient content of the egg) determines caste differentiation. Although based on studies of parasitic Hymenoptera, this hypothesis may prove to be a suitable " explanation " for the sequence of castes of an Aculeate colony established by a single queen. The first brood always consists of small workers, those of succeeding broods gradually increase in size, and only after the largest workers have appeared are the queens and males produced."

The theory as applied to *Bombus* in the broad sense would be as follows. During the early stages of colony formation, and prior to male production, the eggs are retained for some time at the bases of the ovarioles before they are laid, during which time the process of oösorption removes something from the eggs. This delay in oviposition assures that the eggs are fertilized so that they produce only females, and oösorption reduces the nutriment of the eggs, which results in the production of small females or workers. As the colony becomes larger this delay in oviposition is reduced, so that finally at the period of maximum oviposition rate eggs are laid without being fertilized and male brood is produced. At this time or later, when we must assume there is a fall in the rate of oviposition, fertilized eggs are again the majority, but these are laid at a rate which eliminates the effects of oösorption.

This is one of many unproven theories which might be put forward as a possible explanation. Reynolds (1945) has shown that parental nutrition produces effects on the rate of development of offspring in the flour beetle, *Tribolium*. The hypothesis that an increasing economy in the nest results in larger and better nourished eggs being laid later in the life of the colony is an example of such an alternative which might be put forward. Such theories are extremely difficult to prove, and the attempt at experimental proof of some more simple explanation would, if such is available, seem to be the first step in tackling the problem.

Flanders' theory involves some features which would be rather difficult to explain both in *Bombus* and social vespids. His suggestions are again considered in a later section.

The present work has followed Wheeler and Sladen in assuming that there is no difference in the egg which produces queen and worker. An attempt has been made to elucidate the facts of larval nutrition, as this would appear to be the basic approach to the subject. The examination of other theories would come as a natural sequence to this. Haydak (1943) has shown the possibility that caste differentiation in *Apis* may be due to the quantity and not quality of larval food.

In the present work it has been assumed that there is no difference in the egg which produces queen and worker. The question then is one of food, concerning type of food and quantity of food.

The type of food has not been studied, so that the importance of such factors as the production of glandular secretions, the malaxation of eggs, and the proportions of honey and pollen, is not known, and in the future the significance of these may be shown.

When we consider the quantity of food, we must regard the mixture of honey, pollen and elaborated substances added as a food which does not vary greatly in its constitution throughout the life of the colony.

If, as is generally supposed, it is the quantity of food which determines which shall be queen and which shall be worker, then it is of interest to study the brood, its nutrition, and changes in worker populations in nests, to see if any mechanism exists whereby greater amounts of food become available for the individual larva.

In studying the quantity of food received we must consider conditions of the average larva and of the individual larva, for, as will be seen later, these latter may vary in the one nest at the same time. Conditions for the adult as well as for the larva must also be considered, but generally speaking, the conditions of one are the conditions of the other, and well-fed larvae will produce adults which emerge into a nest of plenty.

(b) *Method of Nutrition: Its Effect on the Size of Adult Individuals.*

One noticeable feature in any *Bombus* colony is the variation in size of the workers. This is not due to a mixture of old smaller, and young larger individuals. This variation, which is obvious if one studies the size of brood cocoons, persists until the time of production of males and queens. In this connection Sladen (1912) writes as follows: "A larva that happens to lie underneath a large number of others generally has to build its cocoon almost horizontally, so that the end through which the perfect bee will escape may be free. Such a larva often fails to obtain a sufficient supply of food, with the result that it does not grow to full size and develops into a small bee. In this way tiny workers—I have seen some no larger than a house-fly—are sometimes produced, particularly in the nests of 'carder-bees,' who do not feed their young with such care as the underground species."

The reason for variation in size of individuals will no doubt be found rather in a combination of factors than in a single factor.

In the "pocket-makers" the larvae are fed on both bee-bread and a regurgitated honey and pollen mixture, at least in the earlier stages of colonial development. The relationship of larva to bee-bread in the "pocket-maker" *B. agrorum* is as follows: The bee-bread forms a "mushroom" or flattened cone of food which is always thicker at the centre than at its periphery, where it merges into the waxen envelope which covers the larvae lying on the upper surface of the "mushroom" (fig. 1). When the larvae have entered their 4th instar they spin flimsy silken partitions (Sladen, 1912; Frison, 1928, '29, '30*a*), which immobilize them and fix their positions relative to the other members of the group. This occurs early in the 4th instar and before the period of greatest growth. The more successful larval nutrition would seem to be partly dependent upon access to the bee-bread. Such access is often denied the peripheral larvae in the later stages of development owing to the decrease in the amount of bee-bread, the tendency of the workers to deposit it in the centre of the "mushroom," and also owing to the increase in size of the central larvae, which push the outer ones away from the basal food supply. The small cocoons of a single group are invariably peripheral, and these factors would appear to be at least partly responsible for this.

The above may help to explain the variation in "pocket-makers," but it does not explain the variation in species which do not share this mode of larval nutrition.

Some time may elapse between the hatching of the first and last larva in any one egg group. This is probably due to the order of laying, but may also be affected by inherent differences in the egg. In any group of larvae where they can be recognized as such, usually two instars are present. The larvae are also quite active and mobile, and no doubt there is competition for feeding places until such time as they become immobilized by their external bulge in the wax and the inter-larval first-spun partitions. Although each larva is reputed to receive food by separate injection in its more advanced stages, collective competitive feeding amongst mobile larvae of different instars must undoubtedly pave the way for the ultimate variation in size. Uniformity of brood, when food is relatively scarce, will only occur, providing inherent differences in the egg are not great, where individual larvae are isolated from the earliest stages, as in social wasps. In *Bombus* uniformity in size, or an approach to this condition, is more marked in the male and queen brood, which is produced at the climax of the colony. One of the normal features of such nests is the surplus food store.

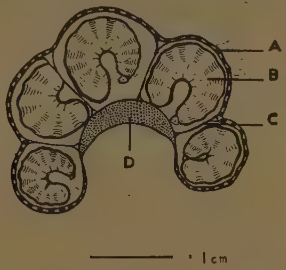


Fig. 1.—Cross section of a brood group from a nest of *Bombus agrorum* (Fabr.) ("pocket-maker"), showing the relationship of fourth instar larvae with the bee-bread. A = external waxen covering; B = larva feeding on D; C = silken partition; D = "mushroom" of bee-bread.

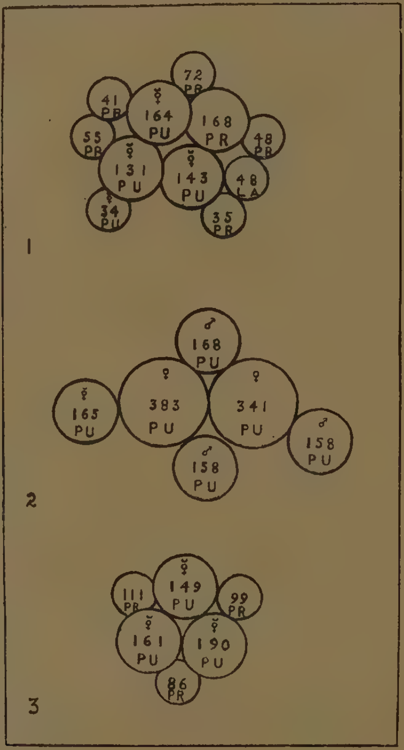
To summarize: Variation in size of workers is caused by possible inherent differences, collective and competitive feeding, and association of individuals of different instars. In one group of humble-bees, the "pocket-makers," the competitive feeding in some species is continued into the later stages of larval life.

Fig. 2 shows the size variation in cocoon groups from species of the "pocket-making" division where the original larval groups tend to remain distinct. In the "pollen-storers" the groups tend to separate, so that one cannot be certain that one is dealing with what was originally a single egg-group.

(c) *The Seasonal Variation in Size of Female Individuals.*

The size of individuals has been measured, using adult weight, wing-length and pupal weight.

Adult weight.—All individuals were weighed alive on an Oertling balance with readings to the nearest mg. Weight as a measure of size of the adult is, however, subject to two obvious errors. Individuals are able to carry 30% of their weight in corbicular pollen, so that it has been necessary to remove this prior to weighing. A considerable weight of honey is carried in the crop of some returning foraging bees. The correlation between weight and some constant such as wing-length is much higher if the foraging bees are not included.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2

Fig. 2.—Diagrammatic representation of brood in groups derived from a single egg-chamber in "pocket-making" species. 1. From a nest of *Bombus ruderarius* (Müll) taken on 9.vii.46. 2. From a nest of *Bombus agrorum* (Fabr.) taken on 19.viii.46. 3. The initial brood group of the queen from a nest of *Bombus agrorum* (Fabr.) taken on 27.v.47. Numbers refer to weight (mg.). PU = pupa; PR = prepupa; LA = larva.

Wing-length.—Measurements of wing-length were made on the left fore wing, the distance from the centre of the tegula to the wing tip being measured to the nearest half mm. A small number of individuals cannot be measured accurately owing to wear of wing tips.

Pupal-weights.—Pupal-weights as an indication of the size of the adult are subject to error in that they do not take into account the loss of weight for

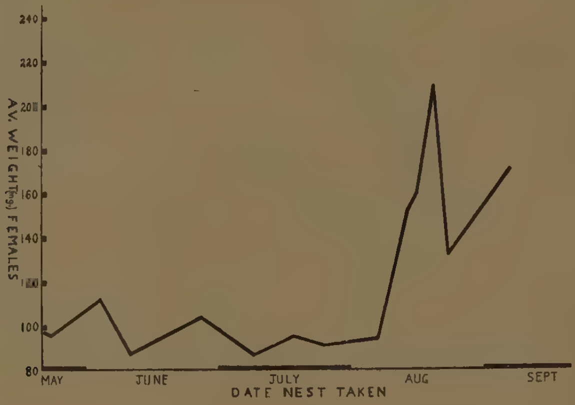
TABLE II.—*Weights (mg.) of Female Bees in Nests of* B. agrorum (" *Pocket-maker* ").

Nest No.	3	4	9	13	19	22	24	25	29	31	33	34	35	36	38 (ii)	39 (iii)	40	41
Date	21.v	22.v	3.vi	10.vi	21.vi	28.vi	2.vii	8.vii	24.vii	6.viii	13.viii	15.viii	19.viii	22.viii	28.viii	3.ix	5.ix	6.ix
No. adults	7	5	7	17	27	8	68	29	11	111	91	98	28	175	168 (i)	141	13	156
20–40	–	–	–	2	–	–	3	1	–	6	–	–	–	3	10	–	–	2
41–60	–	–	–	–	2	1	11	6	1	11	1 (1)	5	1	12	4	4	1	8
61–80	1	2	–	2	3	2	10	5	1	22	8	7	1	20	11	17	5	12
81–100	2	1	2	6	5	2	14	4	3	19	9 (1)	5	–	26	6 (1)	17	3	14
101–120	3	1	2	5	10	2	12	5	4	24	4 (8)	3 (3)	4	31 (1)	2 (8)	17 (2)	1 (1)	13
121–140	–	1	2	1	5	–	8	6	–	16	9 (6)	10 (3)	1 (2)	29 (6)	5 (4)	11 (9)	1	11 (1)
141–160	–	–	–	–	–	–	6	1	1	7	8 (3)	17 (1)	3 (1)	14 (5)	2 (2)	10 (4)	1	13 (1)
161–180	–	–	–	–	1	–	2	–	1	4	9 (3)	13 (2)	–	5 (1)	2	4 (1)	–	16 (1)
181–200	–	–	–	–	–	–	1	–	–	–	6	9	3	3	1	1	–	12
201–220	–	–	–	–	–	–	–	–	–	1	6	5	2	2	1	1	–	4
221–240	–	–	–	–	–	–	–	–	–	–	3	5	2	2	4	1	–	4
241–260	–	–	–	–	–	–	–	–	–	–	–	3	–	–	7	–	–	4
261–280	–	–	–	–	–	–	–	–	–	–	3	1	2	–	5	2	–	1
281–300	*	–	–	–	–	–	–	–	–	–	–	–	2	3	7	1	–	7
301–320	–	–	–	–	–	*	–	–	–	–	1	1	1	–	3	7	–	5
321–340	–	–	*	*	*	–	*	–	–	–	1	1	–	–	1	10	–	8
341–360	–	–	–	–	–	–	–	–	–	–	–	1	1	*	–	9	–	5
361–380	–	–	–	–	–	–	–	*	–	*	*	1*	1	4	–	1	–	5
381–400	–	–	–	–	–	–	–	–	–	–	–	–	–	4	–	1	–	6
401–420	–	–	–	–	–	–	–	–	–	–	–	1	1	2	–	2	–	–
421–440	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4	–	–
441–460	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	2	–	2
461–480	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	–	–

(i) Those dying during experiment not represented here.
(ii) Fed sparingly for 5 days in captivity before weighing.
* Original queen.

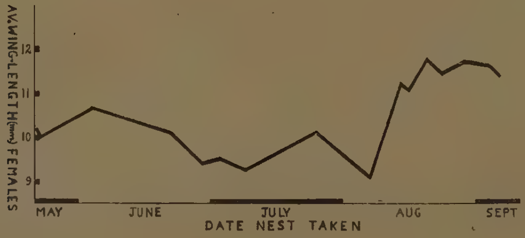
(iii) Kept with a surplus of honey and pollen in captivity for 6 days before weighing.
Males in brackets.

the particular stage of pupation, but a normal nest has pupae in all stages of development, so that the average weights of pupae in nests, considered amongst themselves, would seem to be of some value in assessing seasonal trends.



3

Fig. 3.—Average weight (mg.) of female bees (excluding the original queen) in nests of *Bombus agrorum* (Fabr.) taken during 1946.



4

Fig. 4.—Average wing-length (mm.) of female bees (excluding the original queen) in nests of *Bombus agrorum* (Fabr.) taken during 1946.

(1) The "Pocket-Makers."

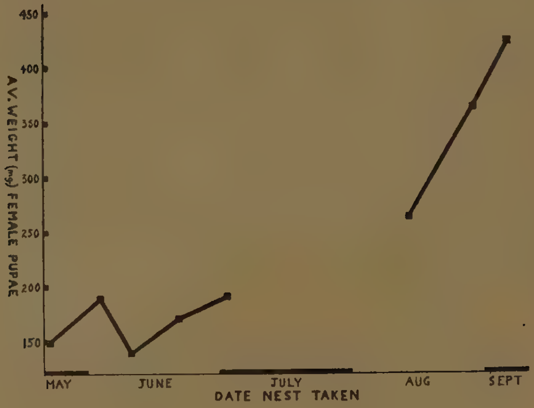
During 1946 nests of *B. agrorum* were studied to obtain data. Table II shows the frequency distribution by weight of female bees, fig. 3 their average weight. Table III shows the frequency distribution by wing-length of all females, fig. 4 their average wing-length. (The original ♀ is not included in the above.) Table IV shows the frequency distribution by weight of female pupae, fig. 5 their average weight.

TABLE III.—*Wing-lengths (mm.) of Female Bees in Nests of* B. agrorum (“*pocket-maker*”).

Nest .	3	4	9	13	19	22	24	25	29	31	33	34	35	36	38	39	41
Date	21.v	22.v	3.vi	10.vi	21.vi	28.vi	2.vii	8.vii	24.vii	6.viii	13.viii	15.viii	19.viii	22.viii	28.viii	3.ix	6.ix
No. adults .	7	5	7	17	27	8	68	29	11	111	91	98	28	175	168	141	156
5·25 .	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–
5·75 .	–	–	–	–	–	–	–	–	–	3	–	–	–	–	–	–	–
6·25 .	–	–	–	1	–	–	–	1	–	1	–	–	–	–	–	–	–
6·75 .	–	–	–	1	–	–	3	1	–	6	–	–	–	3	1	–	2
7·25 .	–	–	–	–	2	1	3	3	–	3	–	2	1	2	–	2	2
7·75 .	–	–	–	–	–	–	6	2	–	7	3	2	–	4	1	3	5
8·25 .	–	–	–	–	–	1	6	1	1	10	1	2	–	11	2	4	3
8·75 .	1	1	–	1	–	–	2	2	–	12	2	4	1	6	4	2	5
9·25 .	–	–	–	1	4	–	9	3	1	14	3	2	–	13	7	8	10
9·75 .	–	2	1	3	4	3	6	7	–	12	4	5	2	16	2	7	10
10·25 .	2	2	1	5	7	1	11	1	3	20	9 (7)	3 (1)	1 (1)	30 (1)	5	8	9
10·75 .	2	–	2	3	6	1	8	3	2 (1)	10	5 (7)	5 (4)	3	24 (2)	2 (3)	4	8
11·25 .	–	1	2	1	1	–	5	3	1	4	3 (4)	19 (2)	1 (1)	19 (4)	3 (2)	3 (5)	21 (2)
11·75 .	–	–	–	–	2	–	5	1	–	2	12 (2)	20	2	12 (6)	4 (8)	3 (5)	17
12·25 .	–	–	–	–	–	–	1	–	–	2	12	15 (1)	3 (1)	4	2 (2)	2 (1)	16
12·75 .	–	–	–	–	–	–	–	–	–	–	4	3 *	2	4	1	2	6
13·25 .	–	–	–	–	–	–	*	–	–	–	5	2	3	4 *	9	6	11
13·75 .	–	–	–	–	–	*	–	–	–	–	2	2	5	6	13 (1)	15	20
14·25 .	*	*	–	*	*	–	–	*	–	–	–	1	–	3	6	15	7
14·75 .	–	–	*	–	–	–	–	–	–	–	–	–	–	–	–	–	–

Males in brackets.

* Original queen.



5

Fig. 5.—Average weight (mg.) of female pupae in nests of *Bombus agrorum* (Fabr.) taken during 1946.

Table IV.—*Pupal Weights (mg.) of Female Pupae in Nests of* B. agrorum (" *Pocket-maker* ").

Nest	3	9	13	19	24	33	38	39	40	41
Date	21.v	3.vi	10.vi	21.vi	2.vii	13.viii	28.viii	3.ix	5.ix	6.ix.46
No. adults (females)	6	6	16	28	68	89	124	83	12	105
60–80	1	–	3	5	1	–	–	–	(1)	1<60
81–100	1	1	1	1	2	(1)	–	(5)	–	–
101–120	1	–	3	4	2	1 (2)	–	(4)	–	–
121–140	1	–	4	8	2	3 (3)	(2)	(16)	–	–
141–160	4	–	5	4	3	4 (4)	(4)	(10)	(2)	–
161–180	2	–	3	4	6	3 (2)	(11)	(29)	(4)	1
181–200	2	1	1	1	13	3	(10)	(37)	(2)	–
201–220	–	2	–	–	11	(2)	1 (3)	(71)	(3)	1
221–240	–	–	2	–	7	2 (1)	1	(63)	–	–
241–260	–	1	–	–	7	1	–	(27)	–	–
261–280	–	–	–	–	–	1	3	(3)	–	–
281–300	–	–	–	–	–	2	1	–	–	–
301–320	–	–	–	–	–	1	3	–	–	2
321–340	–	–	–	–	–	–	8	2*	–	3
341–360	–	–	–	–	–	2	11	8*	–	3
361–380	–	–	–	–	–	6	17	2*	–	8
381–400	–	–	–	–	–	–	9	1*	–	8
401–420	–	–	–	–	–	4	12	–	–	16
421–440	–	–	–	–	–	–	2	–	–	18
441–460	–	–	–	–	–	–	–	–	–	17
461–480	–	–	–	–	–	–	–	–	–	20
481–500	–	–	–	–	–	–	–	–	–	7
501–520	–	–	–	–	–	–	–	–	–	1
521–540	–	–	–	–	–	–	–	–	–	–

* Unemerged callows. Males in brackets.

(ii) The " *Pollen-storers*."

During 1947 nests of *B. lucorum* were studied. Table V shows the frequency distributions by weight of adult females and female pupae. Table VI shows the frequency distribution by wing-length of female individuals.

TABLE V.—*Weights* (*mg.*) *of Female Bees and Female Pupae from Nests of* B. lucorum (“ *Pollen-storer* ”).

	Adults.					Pupae,		
Nest No. .	10	3	15	25	64	3	15	64
Date ..	13.vi	16.vi	20.vi	25.vi	16.vii	16.vi	20.vi	16.vii
Av. weight of ☿☿ .	138·0	146·3	189·7	159·5	158·0	—	—	—
40–60 .	—	—	—	—	4	—	—	—
61–80 .	4	1	1	1	9	—	—	—
81–100 .	3	2	2	3	16	—	—	—
101–120 .	2	7	4	3	20	3	2	—
121–140 .	1	3	5	3	27	3	—	—
141–160 .	2	8	7	3	24	5	3	—
161–180 .	2	2	14	4	25	7	3	—
181–200 .	3	6	12	4	25	10	1	—
201–220 .	3	1	11	1	10	9	3	—
221–240 .	—	—	9	1	14	3	5	—
241–260 .	—	—	7	—	4	8	2	—
261–280 .	—	—	3	—	6	—	6	—
281–300 .	—	—	1	—	—	—	2	—
301–320 .	—	—	—	—	2	—	2	—
321–340 .	—	—	—	—	—	—	1	—
341–360 .	—	—	1	—	—	—	—	—
361–380 .	—	—	—	—	—	—	—	—
381–400 .	—	—	—	—	—	—	—	—
401–420 .	—	—	—	—	—	—	—	—
421–440 .	—	—	—	—	—	—	—	—
441–460 .	—	—	—	—	—	—	—	—
461–480 .	—	—	—	—	1	—	—	—
481–500 .	—	—	—	—	9	—	—	—
501–520 .	—	—	—	—	8	—	—	—
521–540 .	—	—	—	1	11	—	—	—
541–560 .	—	—	—	3	11	—	—	—
561–580 .	—	—	—	2	3	—	—	—
581–600 .	—	—	—	—	1	—	—	—
601–620 .	—	—	—	—	2	—	—	—
621–640 .	—	—	—	—	3	—	—	2
641–660 .	—	—	—	—	1	—	—	4
661–680 .	—	—	—	—	—	—	—	4
681–700 .	—	—	—	—	1	—	—	6
701–720 .	—	—	—	—	—	—	—	11
721–740 .	—	—	—	—	—	—	—	2
741–760 .	—	—	—	—	—	—	—	—
761–780 .	—	—	—	—	—	—	—	3
>780 .	—	—	—	—	—	—	—	—

Analysis of Data on Seasonal Variation.

“ Pocket-makers.”

The study of the seasonal variation of female individuals in nests of *B. agrorum* using adult weight, wing-length and pupal weight as measures of size, shows that the average size of the individuals falls slightly from the first emergence during the middle of May till the second week in August, when there is a sudden rise marking the onset of queen production. In this species, the production of queens is not the result of a gradual increase in the average size of workers such as has been claimed by writers for other species, although there may be a tendency for some workers to be larger as the season progresses. The factors responsible for this sudden change to queen production would not

TABLE VI.—*Wing-lengths (mm.) of Female Bees in Nests of* B. lucorum (“*Pollen-storer*”).

Nest No.	3	15	25	64
Date	16.vi	20.vi	25.vi	16.vii.47
No. adults	30	75	29	227
6·75	—	—	—	—
7·25	—	—	—	4
7·75	1	1	1	9
8·25	—	—	1	6
8·75	1	2	1	11
9·25	3	—	1	9
9·75	5	1	2	9
10·25	1	5	3	11
10·75	4	3	1	10
11·25	10	2	2	17
11·75	4	8	2	26
12·25	1	15	8	28
12·75	—	17	1	17
13·25	—	15	—	12
13·75	—	6	—	4
14·25	—	—	—	—
14·75	—	—	—	—
15·25	—	—	—	1
15·75	—	—	—	9
16·25	—	—	—	39
16·75	—	—	2	5
17·25	—	—	3	—
17·75	—	—	1	—
18·25	—	—	—	—

on the surface appear capable of any simple explanation such as a gradual change in the economy of the colony.

Since the seasonal picture is not one of gradual increase in the average size of workers, it is of interest to determine what changes do take place in the worker population prior to the production of the sexual forms. For this purpose

TABLE VII.—*Wing-length Data from Nests of* B. agrorum.

Nest No.	Date.	☿☿ taken.	Number vacated cocoons.	Average W.L. (mm.) ☿☿	σ.	V.
3	21.v.46	5	7	10·15	·7349	7·24
4	22.v.46	6	11	10·00	·7483	7·48
9	3.vi.46	6	19	10·66	·6481	6·08
13	10.vi.46	16	36	9·69	1·3856	14·30
19	21.vi.46	26	74	10·07	1·1832	11·77
22	28.vi.46	7	25	9·39	1·1832	12·23
24	2.vii.46	65	125	9·51	1·4177	14·78
25	8.vii.46	26	86	9·28	1·4832	15·89
29	24.vii.46	8	52	10·12	·9487	10·12
31	6.viii.46	107	234	9·12	1·3565	14·74

Number vacated cocoons.	Number of nests.	Average σ.
0–20	3	·7104
21–40	2	1·2844
41–80	2	1·0659
>80	3	1·4191

the stage of development of the nest is based on the number of vacated cocoons and the number of workers present.

Table VII shows wing-length data, Table VIII data on pupal weights for nests of different sizes, with analyses of these.

TABLE VIII.—*Pupal Weight Data from Nests of* B. agrorum.

Nest No.	Date.	☿☿	Vacated cocoons.	Average weight (mg.) pupae.	σ.
3	21.v.46	5	7	148·4	31·83
9	3.vi.46	6	19	188·2	61·33
13	10.vi.46	16	36	139·0	44·03
19	21.vi.46	26	74	125·6	106·30
24	2.vii.46	65	125	191·5	42·27

Number of vacated cocoons.	Number of nests.	Average σ.
1–20	2	46·58
>20	3	64·20

Although it is by no means proved that individuals of the first two brood groups (0–20 vacated cocoons) are less variable than subsequent individuals, it is shown that surviving individuals of the first two brood batches are less variable ($P < \cdot 01$). The variation in the size of female pupae from nests shows less variation where there are fewer than 20 vacated cocoons, but data are insufficient for statistical significance. These first two broods are nourished mainly by the queen, which may account for their less variable size; the combination of queen and worker foraging may be more efficient than the first stages of the nutrition of larvae solely by workers. There is also the question of numbers of individuals in these early brood batches.

If some larger workers are produced as the nests increase in size and the average size of workers does not increase, then there must be an increase in the numbers of smaller individuals. It is possible that the temperature and general economy of the nest may govern the size of surviving individuals. Table IX shows the percentage of workers with a wing-length of less than 9·5 mm., and the average wing-length in nests of different sizes as indicated by the numbers of workers present. This confirms an increase in numbers of smaller individuals as the season progresses.

TABLE IX.—*Wing-length less than* 9·5 *mm. in Nests of* B. agrorum.

Number of ☿☿ in nest.	Number of nests.	Percentage W.L. <9·5 mm.	Average W.L. (mm.).
0–10	5	15·5	10·06
11–20	1	25·0	9·69
21–40	2	32·5	9·67
41–80	1	43·0	9·51
>81	1	58·0	9·12

Thus during the expansion of the colony it would appear that food balance in the nest is even more precarious than in the earliest stages of colonial development and that such a condition tends to increase the numbers of small individuals, but the development of a small number of large workers occurs.

"Pollen-storers."

Data from nests of "pollen-storers" are insufficient for analysis on the same scale as in the "pocket-makers." The study of the seasonal variation of adult females in nests of *B. lucorum* shows, however, that although the average weight of workers in queen-producing nests is higher than in nests not producing queens, the difference is not statistically significant.

The seasonal variation would appear to be similar to that shown in the "pocket-making" species *B. agrorum*, i.e. there is no seasonal increase in the average size of workers, although some larger individuals and an increased number of smaller individuals are produced later in the season.

It is obvious in this "pollen-storing" species that there is no question of a gradual increase in size of workers, with an ultimate mergence with queen production.

(d) *A Division of Labour.*

(i) "*Nurse-bees*" *and* "*Foragers.*"

The economy in a colony may be increased not only by an increase in available labour, but also by division of labour. For example, it is doubtless more economical that larger individuals should forage, and that the smaller ones should do the "housework." Coville (1890) was one of the first investigators to hint at such a division of labour. He writes as follows concerning the "pocket-maker," *B. borealis* Kirby: "The precise functions of the different-sized workers were not evident, but in general the larger ones attended to the mending of the grass covering of the nest and to the bringing in of honey, while the smaller ones for the most part did the inside 'housework,' the wax patching, and the nursing described below. The nursing, indeed, was never done, so far as was observed, by a large or even a medium-sized bee."

Richards (1946) recognized this division of labour into larger foragers and smaller individuals which remained in the nest. He writes: "The analysis of workers clearly shows that the fresher workers are larger, suggesting a progressive change with the development of the colony. This is best shown in those captured in the nest. The foragers, on the other hand, are larger individuals, and the data suggests a division of labour. The smaller workers, which are quite common in the nest, resemble foraging workers of the first brood, but later in the season they probably devote themselves mainly to nursing and nest construction" (*B. agrorum*).

For the purpose of obtaining data on the division of labour, worker bees have been divided into two groups, namely "nurse-bees" and "foragers." Those bees which are taken in the nest have been classed as "nurse-bees," and those which return to the nest site have been called "foragers." Some "foragers" which happen to be in the nest will be included with the "nurse-bees," and escaping "nurse-bees" will be classed as "foragers." Success in the determination of the significance if this division of labour is thus dependent upon weather conditions and upon the success with which the nest is taken.

During 1946 it was found that the use of wing-length, hamuli number, and weight as measures of size, all provided significant evidence of a division of labour. However, in view of the fact that no new information was obtained from the study of the hamuli number, and that weight measurements are subjected to considerable error unless there is a standardization of feeding conditions, only wing-length data are submitted here as evidence for this division of labour.

The wing-length of " nurse-bees " and " foragers " has been measured in nests belonging to both " pocket-makers " and " pollen-storers."

Data from " Pocket-makers."

Table X shows the average wing-length of " nurse-bees " and " foragers " taken from nests of *B. agrorum* during 1946. The difference in nests 33–36, 41, shows significance (<P·01). The difference in average size of these two groups of workers is seen to be larger in nests producing males and queens.

TABLE X.—*Wing-lengths (mm.) of " Nurse-bees " and " Foragers " in Nests of* B. agrorum *(" Pocket-maker ").*

Nest No. . .	19	24	25	31	33*	34*	35*	36*	41*
Date . . .	21.vi	2.vii	8.vii	6.viii	13.viii	15.viii	19.viii	22.viii	6.ix
Average W.L. of all ☿☿ .	(26) 10·07	(66) 9·51	(28) 9·28	(111) 9·12	(60) 11·03	(81) 11·04	(17) 10·93	(147) 10·16	(112) 10·59
Average W.L. of " nurse-bees " .	(20) 9·95	(43) 9·23	(25) 9·21	(91) 8·97	(37) 10·28	(51) 10·70	(9) 10·25	(93) 9·71	(80) 10·24
Average W.L. of " foragers " .	(6) 10·41	(23) 10·30	(3) 9·90	(20) 9·85	(23) 12·25	(30) 11·60	(8) 11·69	(54) 10·93	(32) 11·47

* Nests producing queens.
Number of specimens shown in brackets.

Data from " Pollen-storers."

Table XI shows the average wing-length of " nurse-bees " and " foragers " in nests of bees belonging to the " pollen-storers " taken during 1947. The division of labour is shown to be significant in nests of *B. lucorum* and *B. terrestris* (P<·01) in nest 64 and nest 49.

TABLE XI.—*Wing-lengths (mm.) of " Nurse-bees " and " Foragers " in Nests of the " Pollen-storers."*

Nest No. . .	3	15	35*	25*	64*	71*	49*
Date . . .	16.vi	20.vi	23.vi	25.vi	17.vii	22.vii	31.vii
Species . .	*lucorum*	*lucorum*	*pratorum*	*lucorum*	*lucorum*	*lapidarius*	*terrestris*
Average W.L. of all ☿☿ .	(30) 10·60	(75) 12·23	(41) 9·73	(31) 11·15	(173) 11·02	(42) 10·65	(83) 12·30
Average W.L. of " nurse-bees " .	(22) 10·48	(68) 12·21	(20) 9·40	(23) 10·95	(96) 10·42	(65) 10·72	(52) 11·44
Average W.L. of " foragers " .	(8) 10·94	(7) 12·39	(21) 10·04	(8) 11·63	(77) 11·78	(77) 10·60	(31) 13·75

* Nests producing queens.
Number of specimens shown in brackets.

TABLE XII.—*Mentum Lengths of Workers of* B. agrorum *Visiting Flowers of Different Species.*

Sample.	Date taken.	Locality.	Species of flower.	Number of specimens.	Average mentum length	Mentum range.	σ.
1	12.viii.47	Staines	*Solanum dulcamara* L.	11	340	312–362	17
2	10.viii.47	,,	*Ballota nigra* L.	20	341	301–391	26
3	10.viii.47	,,	*Calystegia sepium* (L.) R. Br.	20	358	314–393	21
4	13.viii.47	Sunninghill	*Lotus corniculatus* L.	12	336	275–397	38
5	15.viii.47	,,	*Erica cinerea* L.	12	280	252–329	21
6	15.viii.47	,,	*Cirsium palustre* (L.) Scop.	10	328	285–399	31
7	14.viii.47	Slough	*Ballota nigra* L.	12	331	301–362	20
8	14.viii.47	,,	*Lamium album* L.	13	300	248–340	27
9	14.viii.47	,,	*Trifolium pratense* L.	11	347	303–393	28
10	14.viii.47	Harmondsworth	*Symphytum officinale* L.	12	376	345–413	20
11	20.viii.47	,,	*Epilobium hirsutum* L.	11	311	268–365	32

Values of " P " for Nos. 7, 8, $< \cdot 05$; 10, 11, $< \cdot 01$.

This division of labour is thus shown to be a significant phenomenon. Its significance is dependent upon variation in the size of the worker individuals, and is more easily shown at the climax of nests. It may also occur in younger nests, but here significance is more difficult to obtain on account of the smaller number of bees, and in addition, it has been shown that there is less variation in the size of workers in newly founded nests of some species.

The smallest workers often have malformed wings so that they are forced to remain in the nest. It is probable, however, that a large number of small individuals rarely leave the nest. In the earliest stages of colonial development and during the stage of dying out these smaller workers are often forced to forage, so that one does occasionally see these tiny individuals on flowers.

Further evidence for this division of labour is provided by records of parasitization by Conopid flies which attack workers while foraging.

(ii) *A Further Division of the "Foragers."*

Just as size has rendered smaller individuals of use in nursing—they are able to move more readily through the intricate galleries of the nest—size of the bees also governs their ability to reach the nectaries of different flowers, for a close correlation exists between length of tongue and size of bee. Table XII provides evidence that different sized "foragers" tend to visit flowers of different species where these are found growing in the same neighbourhood. Figures are in micrometer eye-piece units—1 mm. = 140 units—and refer to mentum lengths.

It might be said that a further division of labour may occur in the "nurse-bees" where some of these have commenced laying eggs.

(e) *The Development of Ovaries in Workers.*

Under certain conditions the ovaries of workers may develop. The eggs laid are presumed to be haploid, and individuals produced from these eggs are apparently normal males.

Some evidence of the factors inducing such ovarial development has been collected.

It is convenient to have some method of measuring ovarial development on a numerical basis. The ovarioles of *Bombus* are polytrophic. If a succession of eggs is followed upwards from the base of the ovariole, a well-defined point is reached where the size of the egg approximates to that of the group of nurse cells adjacent to it. In aqueous dissections the ova are readily distinguishable from the nurse-cell groups by their more opaque appearance. This distinction is not readily observable in alcoholic dissections.

The sum-total of eggs in ovaries which are the same size or larger than the overlying nurse group gives a numerical estimate of the extent of ovarial development (fig. 6). This is the value indicated by "Number of Eggs" in tables following.

Before ovarial development has reached a stage which we can measure by the above method an earlier stage may be recognized, and this can be described as a "filling-out" of the ovariole.

Table XIII summarizes data from the dissection of worker-bees in nests of the different species which were taken during 1946, 1947. Table XIV summarizes data from the dissection of workers taken while foraging (1946).

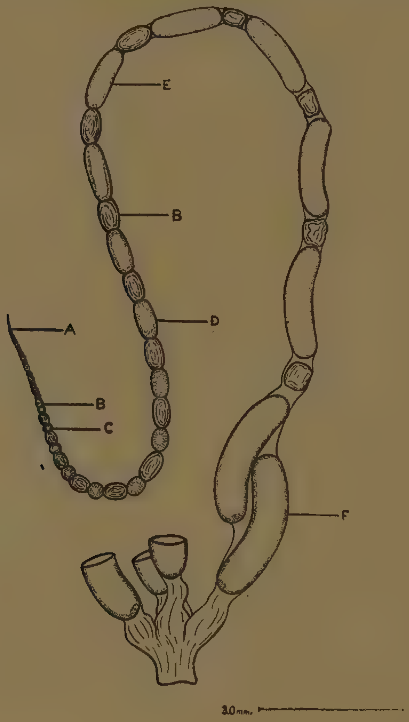


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Fig. 6.—To show method of obtaining egg count in *Bombus* ovaries. All eggs equal to or larger than the nurse-cell group immediately preceding are counted. The count for the ovariole here is 10. A = terminal filament; B = nurse-cell group; C = rudiment of egg; D = last egg to be counted; E = developing egg; F = ripe egg.

Table XIV.—*Development of Ovaries in Workers taken Foraging*, 1946.

Species.	Specimens with ovarial development.	Period found.	Total number of eggs.	Average number of eggs.	Range in egg numbers.
B. agrorum	6	1.vii.46–30.viii	36	6·0	3–10
B. ruderarius	3	12.vii–12.viii	8	2·6	2–4
B. hortorum	9	12.vii–29.vii	90	10·0	6–25
B. lapidarius	4	12.vii–12.viii.46	18	4·5	2–7

Certain facts become evident from the study of the above tables. The life of the normal colony may be divided into two periods, that before, and that after the laying of the eggs which produce sexual forms. During the earlier

Table XIII.—*Development of Ovaries in Workers from Nests taken during* 1946–47.

Date.	Species.	Total ☿☿ in nest.	Number of ☿☿ dissected.		Total number of eggs.		Original female pres.	*Psithyrus* female pres.	Honey stored.	*Brachycoma* infection.
			Nurse-bees.	Foragers.	Nurse-bees.	Foragers.				
25.vi.46	*B. hortorum**	9	9	—	Many	—	+	—	+	++
28.vi.46	*B. hortorum*	13	10	—	138	—	—	*P. barbutellus*	+	++
2.vii.46	*B. agrorum*	68	43	24	—	—	+	—	++	—
8.vii.46	"	28	25	3	—	—	+	—	+	+
9.vii.46	*B. ruderarius**	6	6	—	—	—	+	—	—	—
15.vii.46	*B. hortorum*	26	?	?	114		—	—	++	+++
19.vii.46	*B. lapidarius*	101	24	24	71	—	—	Dead *P. rupestris*	+++	+
24.vii.46	*B. agrorum*	10	8	2	47	—	—	—	+++	+
26.vii.46	*B. ruderarius*	9	7	2	29	—	—	—	+	++
6.viii.46	*B. agrorum*	111	25	20	—	—	+	—	?	+
12.viii.46	*B. lapidarius*	7	5	2	1	—	—	Dead *P. rupestris*	—	—
13.viii.46	*B. agrorum*	62	12	12	—	2	+	—	?	+
15.viii.46	"	82	12	12	3	—	+	—	+++	+
19.viii.46	"	17	9	8	17	3	—	—	—	—
6.ix.46	"	112	9	9	—	—	+	—	+++	?
16.vi.47	*B. lucorum*	30	18	3	—	—	+	*P. bohemicus*	+	—
20.vi.47	"	77	18	5	14	—	+	—	+	—
25.vi.47	"	37	2	—	20	—	—	—	—	+
17.vii.47	"	173	18	12	36	—	+	—	+++	+
22.vii.47	*B. lapidarius*	142	12	12	141	—	—	—	+++	+++
6.viii.47	*B. terrestris*	124	12	12	20	—	+	—	++	++
4.ix.47	*B. humilis*	38	10	28	—	—	+	—	++	++
9 ix.47	*B. sylvarum*	16	13	3	—	—	+	—	—	++

* All bees taken within nest.

period there is no ovarial development in workers providing the original queen is present. If, however, the queen dies during this period, a number of workers will commence laying, and in this way males are often produced much earlier than in the normal nest. During the later period of colonial development, if we exclude the period of dying out, the death of the original queen will also result in egg-laying by workers. This may occur on quite a large scale, when egg-chambers are sometimes unusually large and may contain over forty eggs, indicating that they are used by several workers. But it is apparent that workers may commence laying quite early during the second period, even in the presence of the original queen. This has been shown to occur in *B. lucorum*, *B. terrestris*, and to a lesser extent in *B. hortorum* and *B. agrorum*, where dissection of the original queen showed that she was still laying at a moderate rate, and there is no reason to suppose that males are not sometimes produced in this manner.

It is thus seen that in all stages of colonial development the death or removal of the queen will initiate egg-laying in workers. In the presence of the queen, this habit will only occur in the later stages of colonial development.

A somewhat similar state is known to exist in social wasps of the genus *Polistes*. Pardi (1942) has shown that the factors governing the development of ovaries in workers are quite complex. Here the phenomenon is not dependent solely on size of the worker, but rather on a combination of age and size. It has been found that in *Bombus* it is usually the middle-sized or smaller individuals which develop ovaries. This may be due to the fact that the smaller bees, through a division of labour, stay in the nest, and also live longer. But the explanation may not be as simple as this, for in *B. lapidarius* the tendency is rather for the larger workers to commence laying, but this is the only species in which this has been observed.

Deleurance (1946) has claimed that a psychological relationship exists between queen and worker in *Polistes*, and the same might well apply in *Bombus*. It would thus appear that later in the life of the colony, either due to increase in size of the nest, or to a lessening of ovarial activity and an increasing debility of the queen, this psychological relationship is relaxed.

The fact that there may be no egg-laying in workers in nests where there is a considerable reserve of food, indicates that ovarial development in workers is not primarily dependent upon the relaxing of the conditions of "nutricial castration."

4. THE PRODUCTION OF QUEENS.

(a) *Differences between Queen and Worker.*

(i) *Structural Differences.*

In *Bombus* there are no marked structural differences between queen and worker such as are found in the other genera of the Apoidea which have well-developed social habits. In a few species of *Bombus*, however, there are certain colour differences, and these are usually more marked early in the life of the colony. In *B. terrestris* the pile on the last few segments of the abdomen in workers of the first brood is almost white, whereas that of the queen is a definite buff colour, so that it is difficult to separate the workers from those of *B. lucorum*. A careful examination, however, will show the presence of a thin band of buff-coloured hairs between the white ones and the black ones. Later in the season, however, the colour (especially in the larger workers) comes to resemble that of the queen. Plath (1934) records colour differences for queen and worker of another " pollen-storing " species, *B. affinis* Cresson.

(ii) *Size.*

Generally speaking, the queen is larger and heavier than the worker. In the " pollen-storing " division this is undoubtedly so. In the " pocket-making " division workers as large as fertilized individuals do sometimes occur in the one nest. It seems probable that there is less chance of such individuals hibernating successfully and founding colonies, and this is not a common occurrence.

(iii) *Fat-bodies.*

Perhaps the most outstanding difference between queen and worker is the nature of the fat-bodies, and on this character it is quite easy to separate the two providing they are not callows. When the abdominal cavity is opened, one finds either the tightly packed, pure white fat-bodies such as may be seen in the hibernating queen, or the sparse yellowish fat-bodies of the typical worker. In the queen the abdominal organs tend to be hidden beneath this reserve material. It is easy to tell which is the original queen on the colour of the fat-bodies alone. These are still moderately developed, but they have taken on a brownish appearance, due to specks of a darker substance which are scattered between the cells.

When the new queen emerges from its cocoon, its fat-bodies, like those of the worker callow, are not well formed, but consist of watery tissue with white spherical lumps scattered through the substance. During the first few days of emergence the queen callow feeds heavily, and the characteristic fat-bodies are soon formed. It appears that all individuals with these highly developed fat-bodies are capable of fertilization, even if the reverse is not always true.

(iv) *Time of Production.*

The queens are produced late in the life of the normal colony. They may be produced as much as a month before the normal appearance should the untimely death of the original queen occur. In sub-arctic regions it is probable that on account of the reduced season this difference is not so marked, and the ratio of queens to workers (Richards, 1927) is high at all times. Once the *main* queen brood has been produced, there is no return to worker brood.

(v) *Fertilization.*

The queen is normally fertilized. Several hundred dissections of spring queens have shown 100% fertilization in *Bombus*. It is probable that the size factor is one rendering fertilization of the average worker impossible, but in the " pocket-making " species, where large workers are produced and there is a considerable variation in the size of males, the fertilization of workers does sometimes occur, as is seen in the following nest.

On 26th June, 1947, a nest of *B. hortorum* which had been dug out by a badger was located. The nest material had been pulled together by the workers, but no brood was present. The original queen (572 mg.), one fertilized new queen (455 mg.), and nine workers (109–249 mg.) were present. The spermatheca of one worker (231 mg.) contained motile sperm. The fat-bodies were typically those of a worker, and some of the other workers were of greater wing-length.

In several species of *Bombus* dark pigmented patches may be found at the base of the sting sheath in the queens. These are absent in workers and the unfertilized queens. They are caused by the armature of the male copulatory organ, and they are permanent. The species *B. hortorum* and *B. pratorum* show these copulatory scars very well, and it is possible to ascertain whether the queen has been fertilized by withdrawing the sting of the anaesthetized individual.

(vi) *Diapause and Hibernation.*

It would appear that a period of diapause coinciding in part with hibernation is necessary before the queen may develop ovaries. The worker, however, may develop ovaries and lay male-producing eggs without any such delaying period. The queens of some species are produced at the height of summer in conditions ideal for nest-founding, but there is no evidence to show that two generations ever occur in the one year. Frison (1928) " tried to induce young queens to lay eggs and start a colony the same season in which they were produced " without success.

(b) *The Differentiation of Queen and Worker on a Biometric Basis.*

It has been stated (Frison, 1927 ; Plath, 1934) that a complete range of individuals from the smallest worker to the queen may be found in nests, so that at times it is difficult to tell whether one is dealing with a young queen or a large worker. This range has not, however, been examined statistically except (Richards, 1946) in the case of *B. agrorum*.

Table XV.—*Wing-lengths (mm.) of Female Bees from Queen-producing Nests.*

Serial number.	Species.	Nest number.	Date.	Wing-length (mm.).										
				6·25	6·75	7·25	7·75	8·25	8·75	9·25	9·75	10·25	10·75	11·25
1	*B. agrorum*	39	3.ix.46	—	—	2	3	4	2	8	7	8	4	3
2	,,	41	6.ix.46	—	2	2	5	3	5	10	10	9	8	21
3	*B. hortorum*	27	15.vii.46	—	—	—	—	—	—	—	1	—	—	1
4	*B. pratorum*	35	23.vi.47	—	—	2	—	1	2	7	13	17	4	—
5	*B. lucorum*	25	25.vi.47	—	—	—	1	1	1	1	2	3	1	2
6	,,	64	17.vii.47	—	—	4	9	6	11	9	9	11	10	17
7	*B. terrestris*	49	3.vii.47	—	1	—	3	2	3	5	1	7	3	—
8	,,	158	19.viii.47	—	—	—	1	—	5	6	2	4	—	2
9	*B. lapidarius*	71	22.vii.47	—	—	—	—	—	2	11	14	31	32	35

	Wing-length (mm.)															
	11·75	12·25	12·75	13·25	13·75	14·25	14·75	15·25	15·75	16·25	16·75	17·25	17·75	18·25	18·75	19·25
1	3	2	2	6	15	15	—	—	—	—	—	—	—	—	—	—
2	17	16	6	11	21	7	—	—	—	—	—	—	—	—	—	—
3	6	8	2	7	2	2	—	1	1	3	7	—	—	—	—	—
4	—	—	—	13	19	3	—	—	—	—	—	—	—	—	—	—
5	2	8	1	—	—	—	—	—	—	—	2	3	1	—	—	—
6	26	28	17	12	4	—	—	1	9	39	5	—	—	—	—	—
7	4	5	2	13	16	10	6	2	—	—	—	1	3	8	—	—
8	4	12	6	3	6	4	1	—	—	—	—	2	13	8	4	—
9	13	4	—	—	—	—	—	—	—	3	9	4	—	—	—	—

If one uses some measure such as wing-length, and examines adults from nests of different species which are producing queens, then it will be found that the distinction between queen and worker based on size is quite marked in some species, but not clear cut in others; and that it is only in some nests of the "pocket-making" division that there is any difficulty in making the distinction. This may be seen by reference to Table XV, which gives the frequency distribution by wing-length of female bees in queen-producing nests for members of both the "pocket-making" (1–3) and "pollen-storing" (4–9) divisions. In the "pollen-storers," individuals exceeding 1–3 times the average size of workers in the nest are queens.

A differentiation of queen and worker has also been attempted using adult and pupal weight. Table XVI shows the frequency distribution by weight of

TABLE XVI.—*Weights (mg.) of Female Bees in Queen-producing Nests.*

Serial No.	Species.	Nest No.	Date.	20–40	41–60	61–80	81–100	101–120	121–140	141–160	161–180	181–200	201–220	221–240
"POCKET-MAKERS."														
1	*B. agrorum*	33	13.viii.46	—	1	8	9	4	9	8	9	6	6	3
2	,,	34	15.viii.46	—	5	7	5	3	10	17	13	9	5	5
3	,,	36	22.viii.46	3	12	20	26	31	29	14	5	3	2	2
4	,,	38	28.viii.46	1	4	11	6	2	5	2	2	1	1	4
5	,,	39	3.ix.46	—	4	17	16	17	11	10	4	1	2	—
6	,,	41	6.ix.46	2	8	12	14	13	11	13	16	12	4	4
7	*B. humilis*	151	4.ix.46	2	6	14	6	3	3	—	—	—	—	—
8	*B. sylvarum*	126	9.ix.47	—	3	5	3	2	2	1	—	—	—	—
9	*B. hortorum*	16	17.vi.46	—	—	5	3	7	8	2	6	4	—	—
10	,,	27	15.vii.46	—	—	1	—	—	3	4	8	8	—	2
"POLLEN-STORERS."														
11	*B. pratorum*	10	5.vi.46	—	1	3	6	3	2	1	—	—	—	—
12	,,	17	19.vi.46	—	1	4	13	15	2	—	—	1	—	1
13	,,	35	23.vi.47	—	3	6	14	17	10	—	1	—	—	—
14	*B. lucorum*	25	25.vi.47	—	—	1	3	3	3	3	4	4	1	1
15	,,	64	17.vii.47	—	4	9	16	19	28	24	24	26	9	14
16	*B. terrestris*	49	31.vii.47	—	—	2	7	5	7	6	3	5	5	6
17	,,	158	19.viii.47	—	1	—	5	11	1	3	6	4	4	5
18	*B. lapidarius*	71	22.vii.47	—	—	2	20	34	32	26	8	6	9	5

	241–260	261–280	281–300	301–320	321–340	341–360	361–380	381–400	401–420	421–440	441–460	461–480	481–500	501–600	601–700	701–800	801–900	901–1000	>1000
"POCKET-MAKERS."																			
1	—	3	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—
2	3	1	—	1	1	1	1	—	1	—	—	—	—	—	—	—	—	—	—
3	—	—	3	—	—	—	4	4	2	—	1	—	—	—	—	—	—	—	—
4	7	5	7	3	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—
5	—	2	1	7	11	8	1	1	2	4	2	3	—	—	—	—	—	—	—
6	4	1	7	5	8	5	5	6	—	—	2	—	—	—	—	—	—	—	—
7	1	—	—	2	—	1	2	1	1	—	—	—	—	—	—	—	—	—	—
8	—	1	1	1	—	3	—	—	—	1	—	—	—	—	—	—	—	—	—
9	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—
10	2	1	—	—	—	—	1	—	2	2	3	3	2	1	1	1	—	—	—
"POLLEN-STORERS."																			
11	—	1	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—
12	—	1	—	—	1	—	2	—	—	—	1	—	—	—	—	—	—	—	—
13	—	1	2	10	7	8	3	3	2	1	3	—	1	—	—	—	—	—	—
14	—	—	—	—	—	—	—	—	—	—	—	—	—	6	—	—	—	—	—
15	4	5	—	2	—	—	—	—	—	—	—	1	9	34	7	1	—	—	—
16	8	14	4	6	4	7	3	—	—	—	—	—	—	—	—	2	5	4	—
17	4	3	—	2	—	—	—	—	—	—	—	—	—	2	6	15	—	2	1
18	—	—	—	—	—	—	—	—	—	—	—	1	—	7	4	2	2	—	—

female adults in queen-producing nests of "pocket-makers" (1–10) and "pollen-storers" (11–18). Table XVII shows the frequency distribution by weight of female pupae in nests where both queens and worker pupae are present ("pocket-makers" 1–2, "pollen-storers" 3).

From Tables XV, XVI and XVII it would appear that reports of a gradual transition from worker to queen refer for the most part to members of the "pocket-making" division. A member of this group, *B. agrorum*, has been studied to determine the nature and cause of the transition, for it is obvious that the two extremes of the range represent two very different physiological types. Weight measures a physiological state, but its use is subject to error. The young bee is light for its size, whereas the forager returning to the nest with its crop full of honey, is relatively heavy. Weight can thus give the same measure to two individuals of vastly different physiological make-up. It is, however, possible to reduce the effect of these two factors if the individuals we measure are isolated from the brood and are given the same feeding treatment.

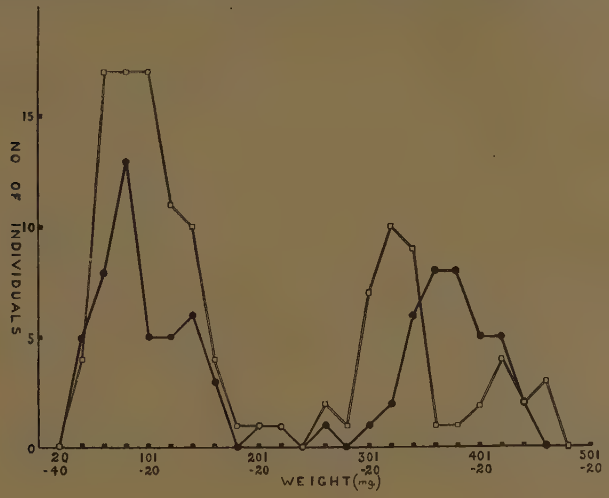
TABLE XVII.—*Weights* (*mg.*) *of Female Pupae in Queen-producing Nests.*

Serial No.	Species.	Nest No.	Date.	100–120	121–140	141–160	161–180	181–200	201–220	221–240	241–260	261–280	281–300	301–320
			"POCKET-MAKERS."											
1	*B. agrorum*	33	13.viii.46	1	3	4	3	3	—	2	1	1	2	1
2	*B. hortorum*	27	15.vii.46	—	—	—	—	—	—	—	—	1	1	—
			"POLLEN-STORERS."											
3	*B. terrestris*	128	6.viii 47	—	1	—	—	1	3	3	3	6	3	5

Serial No.	321–340	341–360	361–380	381–400	401–420	421–440	441–460	461–480	481–500	501–600	601–700	701–800	801–900	901–1000	>1000
				"POCKET-MAKERS."											
1	—	2	6	—	4	—	—	—	—	—	—	—	—	—	—
2	—	—	2	—	—	—	1	—	—	6	21	8	—	—	—
				"POLLEN-STORERS."											
3	3	—	3	1	—	—	—	—	—	1	—	—	7	1	2

Nests which were at the climax of their development were taken. The adults were isolated from the brood in order that no more callows might join them, and food was supplied in the form of honey and pollen which had been gathered from other nests of the same species. Moderate temperatures (20–25 deg. C.) were maintained during experiments. Under these conditions it was hoped that callows would develop normally, and that the effect of the honey in the crop of foragers would be reduced. It was also thought that the physiological make-up of queens and workers would show itself in the stationary position of the worker weight frequency distribution curve, and a corresponding shifting of the queen curve. It was realized that subsidiary factors, such as the state of health of the newly emerged queen and the presence of Conopid larvae in the abdomen of large workers, might still result in a few intermediate individuals of doubtful category. The conditions in each experiment vary, so each is described separately.

Experiment 1.—On 28.viii.46 a nest of *B. agrorum* was taken. The original queen was present, and died during the experiment. All individuals were placed in jars together with comb containing honey, and surviving individuals were weighed on 2.ix.46. By this date the supply of honey was exhausted. Fig. 7 shows the frequency distribution by weight of individuals before and after the treatment. It is obvious that there has been more mortality amongst workers than amongst queens. The average weight of the workers has altered little, but that of the queens has obviously increased.



7

Fig. 7.—Frequency distribution by weight (mg.) of female individuals before = □——□ and after = ●——● feeding treatment in a nest of *Bombus agrorum* (Fabr.).

Experiment 2.—A nest of *B. agrorum* was taken on 3.ix.46. The original queen was missing and workers were laying. Brood was all male except for 13 unemerged queen callows. Adults included 46 workers, 38 queens and 11 males. All female adults were placed in jars with honey and pollen, and surviving individuals were weighed on 9.ix.46. At this time there was still a surplus of honey and pollen. Food was removed, and a further weighing took place 24 hours later. Considerable mortality was associated with the experiment. Results are shown in Table XVIII, where the frequency distributions of weights for the three weighings are given.

These experiments have shown that in the "pocket-making" species *B. agrorum* it is possible to widen the gap between the peaks of this bimodal frequency distribution of weight. But the intermediate values in the trough, which may be discontinuous at several places on account of the small size of the interval, show that there are still some individuals of doubtful position.

If, however, the individuals in doubt here are dissected, it is evident that we are concerned with two very different physiological types. Those which are workers have the scanty light-yellow fat-bodies typical of all workers, the queens have the white prolific fat-bodies, and the distinction in all cases could not be more striking. It is obvious that the queens here will be relatively heavier, and use of this fact may be made to obtain a further separation.

Table XVIII.—*Weights* (*mg.*) *of Female Bees during Feeding Experiment.*

Nest of B. agrorum.

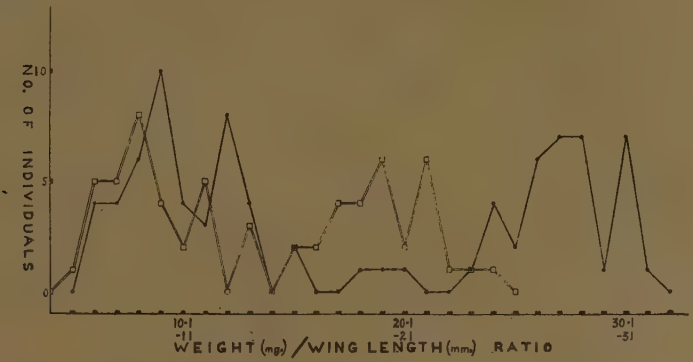
Weight (mg.).	Frequency.		
	3.ix.46.	9.ix.46.	10.ix.46.
20–40	—	—	—
41–60	4	5	1
61–80	17	8	—
81–100	17	13	2
101–120	17	5	4
121–140	11	5	3
141–160	10	6	—
161–180	4	3	1
181–200	1	—	—
201–220	1	1	1
221–240	1	1	1
241–260	—	—	—
261–280	2	1	—
281–300	1	—	2
301–320	7	1	3
321–340	10	2	9
341–360	9	6	8
361–380	1	8	2
381–400	1	8	4
401–420	2	5	5
421–440	4	5	3
441–460	2	2	—
461–480	3	—	—
481–500	—	—	—

Thus, if the frequency distribution of the values weight divided by wing-length is plotted for female adults in nests given the isolation and feeding treatment, a division on a physiological basis may be made. Fig. 8 shows such frequency distribution for two nests of *B. agrorum.*

It is felt that this latter division is more satisfactory than one based on size alone. A few intermediate values still persist. Dissection of these, however, showed that some of the larger workers retained honey in the crop, and that the true division between queen and worker (based on the appearance of the fat-bodies) occurred at the first zero point on the left of the queen peak.

(c) *Brood Data in Nests Producing Queens.*

Brood data from nests which are in the process of changing over from worker to male and queen brood, or in nests which have made this change, have been studied with a view to elucidating the facts of the change. This change-over may not necessarily be the same in different species of *Bombus*. In the "pocket-makers" it is possible to arrange successive batches according to age, and to weigh the brood in such batches, so that some indication of brood changes can be shown; but this cannot be done accurately in the "pollen-storers."



8

FIG. 8.—Frequency distribution of weight (mg.)/wing-length (mm.) ratio in two nests of *Bombus agrorum* (Fabr.) given the feeding treatment.

(i) Analyses in the "Pocket-making" Division.

Nests at the Commencement of Queen Brood.

On 17.vi.46 a nest of *B. hortorum* was dug out from ten inches below a grass tuft. Adults present included the original queen (shown by dissection), 2 new ♀♀ (one escaped, the other weighed 403 mg.), 35 ☿☿ (81–220 mg.), and 12 ♂♂ (100–178 mg.). The brood consisted of 9 batches of eggs totalling 45, 25 1st instar, 18 2nd instar, 18 3rd instar, and 14 4th instar larvae. There were 98 small cocoons containing male pupae and prepupae, and 1 small (worker) and 1 large (queen) cocoon containing female pupae. There were 94 small (worker and male) vacated cocoons and 4 large (queen) vacated cocoons. All the 4th instar larvae and the prepupae were too small to indicate the presence of any further queen brood. The nest had produced five queens (the size of the large cocoons made this very evident) and had returned to male brood. The dissection of the queen showed well-developed ovaries. Workers were not dissected to ascertain if these were laying.

It was easy to trace the cocoon groups from which these early queens had emerged. These were two in number. The first was a group of 20 empty cocoons (8 now containing honey), and comprised 4 large queen and 16 small male or worker cocoons. The second was a group of 13 cocoons. Ten small cocoons were vacated, but the remaining four contained pupae, 2 male, 1 worker and 1 queen. This group shows that during the production of the first queens it is almost certain that eggs which will give rise to queen, worker and male are laid together in the one egg chamber, or at least in chambers so close that the brood subsequently intermingles.

On 2.vii.46 a nest of *B. agrorum* was taken and evidence of the earliest queen production was found. The nest contained the original ♀ and 68 ☿☿, and none of the latter showed any ovarial development. All of the 54 pupae in the nest were female (65–247 mg.). The weights (mg.) of prepupae and 4th instar larvae in their groups were as follows:

Group A. Pupae: 243/181/244/186. Prepupae: 299/252/275/265/241/230.
Group B. Defaecating and spinning larvae: 166/308/402/249/347/228/293/255/337/239/227/191/168/227.
Group C. Defaecating and spinning larvae: 151/190/109/236/109/106/88/84/106/178/167/144/116/96.
Group D. 4th instar larvae: 95/103/89/121/100/95/110/93/55/100/108/120/96.

Group A has typical weights for worker pupae; Group B weights indicate the presence of some queens, and it is here that the change-over is taking place. Unfortunately the sex of these larvae is not known, but the fact that the larvae of Group C, which is the same size as Group B, have finished feeding, and none approaches queen larva weights such as seen in C, indicates, but does not prove, that there has been a change to male brood. In any case it is obvious that a stage where queen production was possible was reached, and this was suddenly curtailed, either by a return to worker brood, by a change to male brood, or a combination of the two.

The Change from the First Appearance of Queen Brood to Purely Queen Brood.

On 13.viii.46 a nest of *B. agrorum* was taken from the side of a grassy clump. The original queen was present (shown by dissection). Adults included 60 ☿☿ (48–237 mg.); 5 ♀♀ (263–333 mg.) and 21 ♂♂. The new queens were not fertilized, but their fat-bodies showed that they were undoubtedly queens, belonging no doubt to the initial change-over group or groups. The weights (mg.) in the brood groups for the different sexes (where this is possible), arranged beginning with the oldest group, were as follows:

Group A. Pupae with pigmented integument:
♂♂ 124/104/148/136/124/103/141.
☿☿ 166/188/188/236/243.
Group B. Pupae with pigmented integument: ♂♂ 145/168/169.
„ white integument and black eyes:
☿☿ and ♀♀ 122/165/110/275/318/172/154/291/345/283.
Group C. Pupae non-pigmented but with black eyes: ♂♂ 83/153.
„ „ „ „ ☿☿ 130/136/143/145/145/193/221.
Group D. Pupae non-pigmented but with black eyes: ♂ 228.
„ „ „ „ ♀♀ 369/409/412/354/367.
Group E. Pupae non-pigmented but with pink eyes: ♂♂ 213/213.
„ „ „ „ ♀♀ 407/420/363/377/377/373.
Group F. Prepupae: 427/420/445/265/231/250/210/175/149/172/220. 4th instar larva 119.

Group G. Prepupae: 317/350/294/325/340/241/218/202/211/145/102/85.
Group H. 4th instar larvae: 473/419/462/382/382/353.
Group I. 4th instar larvae: 444/442/472/363/505/284/547/435/405/346/346/315/278.

This nest illustrates admirably the change-over from initial queen production to a purely queen brood. Several facts may be noted. The change-over here is quite a gradual one, and extends through at least seven larval groups. Female individuals of the size and weight of queens, and males are present in the nest. In the oldest group of pupae (A) we have a mixture of workers and males. In the next group (B) there is a mixture of males, workers and queens. The next group (C) contains males and workers; then comes a group of males and queens. Two groups of prepupae showing weights indicative of male and queen brood follow, then come two groups of 4th instar larvae which are undoubtedly queen brood.

In this data there appears to be some indication that during the change-over from male and worker brood to queen brood, female larvae in smaller larval groups are more liable to be heavier and therefore queens. This is seen in groups D, E and H. It is fairly evident, too, that group C is the last one in which workers will be produced, but in any case G is certainly the last worker-producing group. At this point the economy of the colony is such that all female individuals are reared to queen size.

The Climax Brood of the Normal Colony.

At the climax of the colony the brood is all female, and the size of individuals shows that it is purely queen brood except for the occasional individual, which through some unfavourable circumstance is much reduced in size.

On 6.ix.46 such a nest of *B. agrorum* was taken. The original queen was present. Adults in the nest included 112 ☿☿, 40 ♀♀ and 3 ♂♂. Egg groups were 6/8/11/5/13, and a considerable amount of female brood was present. This has been summarized below to show the constant large size of the individuals, and the relative rarity of small underfed individuals.

Unemerged callows: 383/341/372/349/347/382.
Pupae with pigmented integument: 420/400/421/363/344/322/426/413/452/392/369/398/439/395/201/394/410/456/422/419/403/387/351/387/362/370/402/332/374/403/166/421.
Pupae with non-pigmented integument and black eyes: 313/407/455/452/336/421/485/377/349/452/444/437/382/455/408/439/477/318/435/404/376/450/458/472/404/408/433/440/420/482/472/467/425/417/463/479/419/433/456/481.
Pupae with non-pigmented integument and brown eyes: 461/463/368/437/468/457/453/454/426/466/463/481/437/483/424/474/424/443/470.
Pupae with non-pigmented integument and white eyes: 479/472/493/467/494/445/487/467/427/414/502/474/451/479/444.
Prepupae: 469/447/476/465/459/451/447/478/453/396/423/403/371/476/396/379/482/391/465/479/446/430/270/385/445/349/295/197.
4th Instar larvae: 247/365/584/567/589/481/259/246/481/493/318/635/464/508/439/529/442.

The above nests throw some light on the process of changing over from worker to queen production in nests of species of the "pocket-making" division which were taken from the field. It is possible to describe such a change at least for *B. agrorum.*

Firstly, it is obvious that both male and female-producing eggs are laid together and at the same time, and such laying together of eggs may persist for some period. The fact that normal sized workers and males emerge from one such batch of eggs proves that this association does not necessarily result in immediate advantage for the female-producing egg so associated. The fact, too, that queens and workers are produced from the one batch of eggs, commonly in the earliest stages of queen production and occasionally at the later stage of pure queen production, also points to there being only one kind of female-producing egg. Initially queens may be produced with males and workers, and then there may follow a return to male and worker brood before there is a change to purely queen brood. This shows that it is not a matter of time of laying which determines whether an egg shall develop into queen or worker. It would thus seem apparent that queen production is dependent upon a level of economy in the nest, and that male production tends to associate itself with the commencement of this stage of economy. Once males have been produced, should the economy of the colony fall, rather than return to pure worker production, the tendency is to mix female and male eggs. In this way large workers, queens and males are produced in the one group. Those female larvae which occupy the more favourable central positions in the group develop into queens, and the worker and male brood is peripheral. Eventually, however, the economy of the colony rises above this doubtful level, and male and queen brood emerges. Finally, the male brood is curtailed, and pure queen brood marks the climax of the colony.

(ii) Analyses in the "Pollen-storing" Division.

The examination of the brood at the change-over from worker to male and queen brood is not so instructive in this group of humble-bees, because the batches of larvae derived originally from single egg-chambers do not remain as distinct groups.

The sex ratios of pupae and adults in queen-producing nests of "pollen-storers" are given in Table XIX. From the data it may be assumed that in this group of species the male and queen brood are produced at the same time. There is no evidence that queens are produced before or without males having been produced in nests where the original queen is still alive.

TABLE XIX.—*Pupal Brood in Nests of "Pollen-storers."*

Species.	Date.	Non-pigmented pupae.			Pigmented pupae.			Adults.			Original queen.
		☿☿	♀♀	♂♂	☿☿	♀♀	♂♂	☿☿	♀♀	♂♂	
B. pratorum	5.iv.46	—	10	14	—	2	7	16	1	6	Dead
,,	22.v.46	13	17	2	15	1	—	56	—	—	+
B. lucorum	17.vii.47	—	6	56	—	32	46	186	53	5	+
B. lapidarius	19.vii.47	—	2	30	—	3	19	143	13	6	—
B. terrestris	31.vii.47	—	—	1	—	2	1	92	11	—	+
,,	6.viii.47	4	11	48	28	—	8	120	—	—	+

(d) *Possible Factors in Queen Production.*

(i) *The Brood/Worker Ratio.*

In this connection Richards (1946) has written: "It is usually supposed that the development of males and queens at the end of the nest-cycle is due to an increase in workers which makes it possible to feed the larvae more lavishly. No one, however, appears to have studied the larva/worker ratio, though a record of its changes during the season would seem to bear on the hypothesis. In the present nest (*B. agrorum*) the ratio is 68/153 = 0·44. It is at least clear that these larvae can be better fed than the first brood of larvae, tended by a single queen."

The brood/worker ratio has been studied in three ways, using egg/worker ratio, larva/worker ratio and brood-weight/worker ratio. Table XX gives data from nests of the "pocket-making" species *B. agrorum* taken during 1946. Table XXI gives data from nests of the "pollen-storing" species taken during 1947. Table XXII gives data calculated from a table published by Frison (1930*b*) for natural nests of the "pocket-maker" *B. americanorum*.

Table XX.—*Brood-Worker Data from Nests of* B. agrorum (*"Pocket-maker"*).

Date.	☿☿.	♀♀.	♂♂.	Eggs.	Egg/worker ratio.	Larvae.	Larva/worker ratio.	Mgm. Larval material.	Larval weight/worker ratio.	Original ♀.
21.v.46	6	1	—	15	2·50	18	3·00	1857	309·5	+
22.v.46	5	—	—	?	?	12	2·40	?	?	—
3.vi.46	6	1	—	10	1·67	14	2·33	?	?	+
10.vi.46	16	1	—	37	2·31	22	1·38	4259	266·2	+
21.vi.46	26	1	—	20	0·77	44	1·69	3553	136.7	+
28.vi.46	7	1	—	23	3·29	?	?	?	?	+
2.vii.46	68	1	—	67	0·99	?	?	7691	113·1	+
8.vii.46	28	1	—	29	1·04	38	1·36	?	?	+
6.viii.46	109	1	—	51	0·47	?	?	?	?	+
13.viii.46	62	5	23	38	0·61	47	0·76	17201	277·4	+
28.viii.46	57	28	15	?	?	85	1·49	?	?	—
6.ix.46	112	27	3	43	0·38	45	0·40	24,128	215·4	+

Table XXI.—*Brood-Worker Data from Nests of "Pollen-storers."*

Species.	Date.	☿☿	♀♀	♂♂	Eggs.	Egg/☿ ratio.
					i ii	i ii
B. lucorum	16.vi	30	1	0	45/62	1·5/2·1
,,	20.vi	77	1	0	56	0·73
,,	25.vi	37	6	0	35	0·95
,,	17.vii	186	53	5	43	0·23
B. lapidarius	22.vii	143	13	6	75	0·52
B. terrestris	31.vii	92	11	brood	103	1·12
,,	19.viii	120	25	1 and brood	88	0·73

	Larvae.	Larva/☿ ratio.	Mgm. larval material.	Larval w/t. ☿ ratio.	Original ♀	Laying ☿☿
B. lucorum	19	0·63	4963	165	+, also *P. bohemicus*	—
,,	92	1·20	9591	125	+	—
,,	36	0·97	6167	167	—	?
,,	89	0·48	15025	83	+	+
B. lapidarius	149	1·04	6707	47	—	+
B. terrestris	77	0·84	46987	51	+	+
,,	127	1·06	?	?	+	+

i = *Bombus* values. ii = *Psithyrus* values.

TABLE XXII.—*Brood-Worker Data from Nests of* B. americanorum (“ *Pocket-maker* ”).

Date.	☿☿.	♀♀.	♂♂.	Old cocoons.	Full cocoons.	Eggs.	Egg/ worker ratio.	Larvae.	Larva/ worker ratio.	Pollen pots.
20.vi	0	1	0	0	0	?	—	—	—	—
23.vii	4	1	0	4	15	33	8·25	15	3·75	?
25.vii	44	1	0	78	18	49	1·11	22	·50	12
4.viii	11	1	0	23	8	18	1·63	21	1·91	?
4.viii	17	1	0	45	32	52	3·06	?	—	?
28.viii	7	8	7	50	29	?	—	5	·71	?
6.ix	69	11	10	?	45	?	—	31	·45	19
9.ix	76	57	46	?	101	28	·37	35	·46	16
14.ix	38	21	9	132	34	0	—	0	—	1
13.ix	98	71	25	?	236	4	·04	?	—	18
17.ix	27	25	24	278	80	8	·30	15	56	?
25.ix	13	16	5	192	48	?	—	?	—	?
26.ix	15	?	?	244	10	?	—	34	2·37	?
3.x	10	0	0	?	0	0	—	0	—	?

The life of a colony may be divided into three periods for the purpose of considering brood/worker ratios: (1) The period prior to the production of sexual forms; (2) the period of active production of sexual forms; and (3) the period in which the nest is dying out, and most of the sexual forms have emerged. It is clearly important that the original queen should be present in the nests which are studied, for worker laying, which seems to be initiated more by the absence of the queen than by any other factor, will upset ratios.

We are concerned mainly with changes in the first period, but it is also important to know conditions during the second period. Nests of the third period must not be confused with those of the first period.

Examination of the brood/worker ratio shows that in normal nests there is a decrease in the ratio in period 1 as the season proceeds, although a greater volume of data would be necessary to show the nature of the decrease. The egg/worker and larva/worker ratios in period 2 are, especially in the “ pocket-making ” species, considerably reduced, so that it might well be that there is a relatively sharp drop between these two periods. However, it may be said that the larva/worker and egg/worker ratios must approach or fall below 1 before queen brood is produced.

In Table XX the increase in larval-weight/worker ratio during period 2 is of some interest. This may be due to several factors, such as (1) the production of some larger worker individuals just prior to male and queen brood; (2) a more successful division of labour; (3) utilization of food previously stored in the nest; (4) an increase in the larval period of queen brood.

It would appear that the problem of queen production is concerned basically with the egg-laying rate of the original queen, unless we assume that egg numbers are controlled by workers. This latter fact may well be true, but there is every indication that the egg-laying rate of the queen in the normal nest, whether controlled physiologically or psychologically, follows a definite curve.

The Egg-laying Rate of the Queen.

This has been estimated by several methods using data from nests of *B. agrorum* taken during 1946.

1. *Ovariole counts in queens.*—Counts, as described in the section on ovarial

development in workers, may be made from queens of nests. This will show the condition of the ovaries, but not necessarily the rate of flow of eggs. There is, however, probably a close correlation between the two, and estimates based on this are not influenced by the possible destruction of eggs by workers. No indication of the actual egg-laying rate is obtained in this manner, but relative activity is probably shown. Table XXIII shows average ovariole counts in queens.

TABLE XXIII.—*Ovariole Counts in Queens of Nests* (B. agrorum).

Month.	Number of nests.	Average number of eggs per ovariole.
May	1	0·8
June	3	5·7
July	2	10·0
August	3	8·3

2. *Eggs found in nests.*—The incubation period of eggs is stated by Sladen (1912) and Plath (1934) to be 3–4 days. The average number of eggs in nests taken during the month divided by 4 gives an estimate of daily oviposition rate for this period. Table XXIV shows daily oviposition rates calculated by this method.

TABLE XXIV.—*Estimated Daily Oviposition Rate from Eggs found in Nests* (B. agrorum).

Month.	Number of nests.	Daily oviposition rate.
May	1	3·8
June	5	5·0
July	2	12·0*
August	4	10·8
September	1	10·8

*Estimated oviposition rate in one nest is 16.

3. *Prepupae and pupae in nests.*—The average age of prepupae and pupae may be taken as 15 days, so that a sum total of these divided by 15 gives the daily oviposition rate for a date some two weeks previously, in terms of successful eggs. Nests which are attacked severely by *B. devia* cannot be considered here. Table XXV shows daily oviposition rates calculated in this way.

TABLE XXV.—*Estimated Daily Oviposition Rate from Pupal and Prepupal Brood* (B. agrorum).

Month.	Number of nests.	Daily oviposition rate.
April–May	2	0·9
May–June	3	1·7
June–July	1	4·0
July–August	2	6·6
Aug.–Sept.	2	4·9

4. *Vacated cocoons in nests.*—The average increase in number of cocoons in nests per month divided by 30 gives a viable egg-laying rate for a time 3–4 weeks previously. Table XXVI shows a summary of this data back-dated a month.

Table XXVI.—*Estimated Daily Oviposition Rate from Vacated Cocoons* (B. agrorum).

Month.	Number of nests.	Daily oviposition rate.
April	2	0·3
May	4	1·0
June	3	1·6
July	4	8·8
August	1	0·7

Fig. 9 shows the oviposition rate of the queen during the life of the colony based on the number of eggs, the number of prepupae and pupae, and the number of vacated cocoons found in nests. The period of laying of queen-producing eggs and the period of queen production are also indicated.

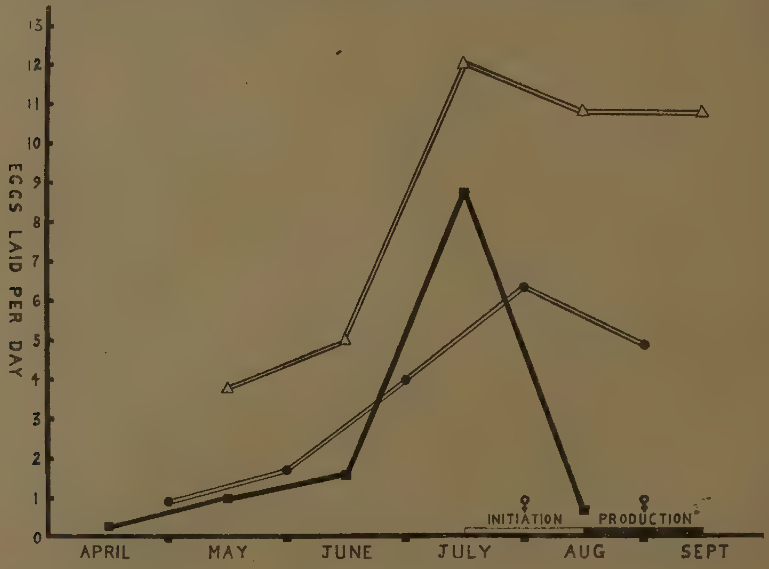


Fig. 9.—Oviposition rate of queens in *Bombus agrorum* (Fabr.) based on 1, △══△ number of eggs found in nests ; 2, ●══● number of pupae plus prepupae found in nests ; 3, ■━━■ number of vacated cocoons found in nests.

The study of Tables XXIII–XXVI shows that the oviposition rate follows a definite curve during the life of the colony. Another obvious feature is the discrepancy between numbers of eggs laid and amount of brood present. It is apparent that at least twice as many eggs are laid as develop into adults.

Observed mortality in egg groups and larval groups would not appear to account for the difference. Reference to Tables XX–XXII, which give egg/worker and larva/worker ratios, also shows this discrepancy between brood produced and eggs laid. Here it is seen that the two ratios are somewhat similar, and in view of the fact that the larval life is about twice the incubation period, the larva/worker ratios are about half what one would expect.

We may assume, then, that for the greater part of the egg-laying period of the queen there is a surplus of eggs laid with which it is possible to maintain a certain balance between economy of the nest and amount of brood. It seems likely that this surplus of eggs is controlled (1) by the queen who lays and attempts to protect them; (2) by the workers who destroy them, so that the number of brood which will be produced is governed by a complex set of conditions. Several writers, including Huber (1802), Sladen (1912) and Plath (1934) have reported that at about the time of laying queen and male-producing eggs the workers will crowd about the queen and often destroy and devour the eggs.

One can at this stage only say that prior to queen production the workers rear relatively fewer and fewer brood until a point is reached, often suddenly, where the ratio is such that the larvae receive sufficient nourishment to develop into queens. It would seem that the individuals in the nest are able by regulation of the numbers of brood to produce workers or queens. If by accident the queen is killed and the regulatory excess of eggs disappears, the workers are unable to control the brood-ratio until such time as some of them develop ovaries and lay eggs, and the last eggs laid by the queen before her death may, under such circumstances, develop into queens (see account of nest below). But in the normal colony the production of queens does not occur till late in its life, and almost invariably is accompanied by the presence of male brood, so that the advent of this male brood would seem to be a signal for a reduction in the brood/worker ratio to that point where queens are produced.

If the production of queen brood in the normal nest is controlled by an inherent psychologically regulated state of economy, then all other factors in queen production become secondary, and are responsible rather for numbers than kinds of individuals produced.

The following nest (referred to above) shows that the death of the original queen early in the season may result in the production of queens. This might well be the result of an inevitable reduction in brood/worker ratio for the last eggs laid by the queen.

On 25.vi.47 a queen-producing nest of *B. lucorum* was taken at Sunninghill, Berkshire. These new queens were far in advance of the normal appearance, for the males in this area did not appear until 11.vii.47. Adults in the nest consisted of 31 ☿☿ (84–227 mg.) and 6 ♀♀ (533–579 mg.). The original queen was found dead in the nest material. The number of vacated cocoons was 38 small and 8 large. Three small cocoons and two large ones contained dead *Brachycoma*-infected pupae. The brood consisted of 35 eggs, 2 1st instar, 11 2nd instar, 6 3rd instar, and 17 4th instar larvae, all of which were male brood from laying workers. No male pupae or prepupae were present, indicating that about two weeks must have elapsed between the death of the original queen and the commencement of worker laying. As only seven small cocoons are not accounted for, and there must have been some worker mortality, it would seem probable that queens had been produced without males. The queen larvae would have stopped feeding by the time that the worker male brood was produced, so that the brood/worker ratio must have temporarily been much reduced.

Perhaps of equal significance was the unsuccessful attempt to produce queen brood early in the life of the colony in the presence of the original queen by the removal of all feeding brood and the leaving of a single egg-group. Two nests of *B. agrorum* were opened at intervals for brood removal, and the history of one of them is summarized in Table XXVII.

TABLE XXVII.—*Attempt to Produce ♀ Brood by Brood Reduction.*

Date of opening.	Brood present.	Brood left.
19.vi.47, est. 15–20 ☿☿	1 group of eggs, 3 2nd, 5 3rd, 7 4th instar larvae, 2 cocoon groups	1 group of eggs, 2 cocoon groups.
26.vi.47	2 larval groups, 1 cocoon group. (Good reserve of honey in vacated cocoons.)	1 larval (1st experimental) group, 1 cocoon group.
16.vii.47	2 groups of eggs, 5 larval groups, 2 cocoon groups. 1st experimental group of 9, obviously ☿ cocoons	1 egg group, 2 cocoon groups.
21.vii.47, est. 20–30 ☿☿	3 egg groups, 1 larval (2nd experimental) group	1 (2nd experimental) larval group, 1 cocoon group.
28.vii.47	2nd experimental group now cocoons (8) and obviously ☿ brood.	

During the above experiment brood/worker ratios such as occur at the time of the normal queen production have been created, but it has been difficult to maintain them because of the ability of the queen to replace brood rapidly. Had the original queen been removed, then the attempt at early queen production might have been successful.

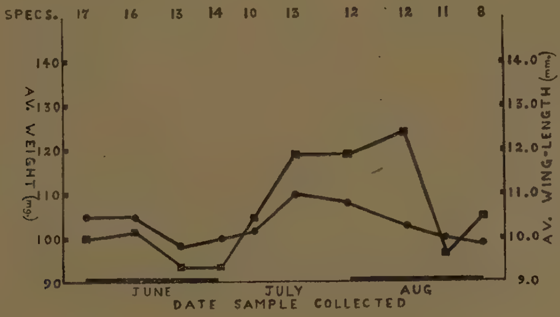
(ii) *The Change from Worker to Male Brood.*

The rate of oviposition of the queen approaches its maximum about the time of laying male-producing eggs. Since the normal queen prepupa is at least about twice as heavy as the male prepupa, there is little doubt that the male larva requires less food. If, as has been shown in *B. agrorum*, the production of queens hangs for a while in the balance, then the presence of male brood may cause the swing to queen production. If, in the rising economy of the nest, there is a change to purely male brood, and there is no marked alteration in oviposition rate, a surplus of food will be stored up in the colony, for the size range of males is more limited by its genetic make-up than is that of the females. The return to female brood under such circumstances will be accompanied by a marked increase in the economy of the colony, with the result that queens are produced. There is little doubt that in *B. agrorum* there are certain stages when the sex ratio of single larval groups will govern whether a female producing egg shall become queen or worker, and this factor might be said to have the same importance as the relative position (central or peripheral) in the larval group of this species. Up till the time of male production the range in weight of female pupal brood in *B. agrorum* is 60–260 mg. After male production, the range of normal female pupal brood is 200–500 mg., which indicates a stabilization in trophic condition.

But the presence of male brood is not an essential factor in queen production, for it has been shown that queens are produced without the presence of this influence. It is at most only a contributing factor in that it affects the amounts of food available and the relative sizes of queen and worker.

(iii) *Increase in Nest Temperature.*

Temperature data have shown that the maximum is reached at the time of production of sexual forms. It seems probable that stable, optimum conditions of temperature result in a shortened pre-adult life, which factor would aid worker increase and therefore the brood/worker ratio. There is doubtless a threshold of temperature below which larvae will not develop into queens, but the fact that a nest may be induced to produce queens a month before these normally would appear, through the death of the original queen, indicates that temperature does not control queen production, but that increased temperature is an accompanying feature.



10

Fig. 10.—Average weight (mg.) = ■═══■ and average wing-length (mm.) = ●━━● of foraging workers of *Bombus agrorum* (Fabr.) taken from the field during 1946.

(iv) *The Availability of Nectar and Pollen.*

Source.—At intervals during the 1946 season foraging bees were collected in the field in order to study seasonal variation in size. They were weighed alive and later wing-lengths were measured. Fig. 10 shows a comparison of these data. The average size of workers varies slightly during the season when measured in wing-length, but the weight has a marked increase. Workers are relatively light in the early part of the season and relatively heavy in the latter part, the change-over occurring early in July. Two factors may be involved in this relative change in weight: (1) there may be a greater amount of reserve material in the worker later in the season; (2) there may be an increased honey load later in the season (pollen was removed before weighing). In either case the result is important. An increase in reserve material means that work is not so exacting, and an increase in honey load means that more food is capable of being transported. The latter is the more likely, but the former cannot be excluded.

Seasonal climatic change.—Increased day temperatures and longer working hours will aid food supply by increasing the load which may be carried, and enabling more trips to be made per day. Krishnamurti (1939) has shown the close correlation between foraging capacity and sunshine, etc., for the honey-bee.

Increase in number of bees foraging.—The increased ease with which nest temperatures are maintained due to increase of brood, and rise in external temperatures, may release more bees for foraging duties. Evidence on this point is very difficult to obtain, because in any one nest the number of bees foraging will depend upon the weather conditions and the state of the colony generally.

Factors affecting availability of food considered here are thought to be general ones which might give a trend to the size of colonies for the particular year, but having little bearing on the mechanism of queen production. Some species of *Bombus* terminate early in the summer, and this suggests that it is a developmental state within the colony which governs queen production.

(v) *The Division of Labour.*

The division of labour which has been shown to occur in several species may well be a contributing factor to the economy of the colony.

(vi) *The Rate of Oviposition.*

In an earlier section reference was made to a hypothesis put forward by Flanders (1945) based on the process of oösorption which is known to occur in parasitic Hymenoptera. The present work contains insufficient evidence to support or disprove this theory. Histological studies would be necessary to show that the process of oösorption does occur, then further detailed estimations of oviposition rates would have to be made. The present indications are that there is, as in *Apis*, a definite oviposition curve with a peak at about the time that the male and first queen producing eggs are laid, after which there is a gradual fall. In *Bombus*, despite this fall, once pure queen brood is produced there is no return to worker brood.

In view of the fact that brood/worker ratios would appear to provide a plausible explanation of caste differentiation in *Bombus*, the first step towards solving the problem would be further experimental work involving brood and worker removals of a similar nature to that performed by Sladen (1912). If a repetition of his work of uniting nests and removing original queens produces new queens from eggs laid early in the life of the colony, and the removal of workers from colonies results in the prevention of queen production throughout the life of the colony, then not only would there be strong evidence for an explanation involving only the *quantity* of larval food, but also there would be good reason to believe that differences in the egg are at most a minor contributing factor to caste differentiation in *Bombus*.

5. Discussion.

The main question concerned in the foregoing is: "What is the factor, or what are the factors responsible for the change from worker to queen brood, and how is this change brought about?"

During the course of the work on *Bombus*, it has become increasingly evident that we are concerned with two groups of species having many different biological characteristics, so that problems have to be considered separately for each group. These groups were called "pocket-makers" and "pollen-storers" by Sladen in 1912.

The "pollen-storers" are generally regarded as the more specialized species, for their larval nutrition resembles more the condition found in more specialized Apoidea in that there is individual larval nutrition for a longer period of larval life. In these species, too, the worker caste is more clearly separated from the queens. In the "pocket-makers" the larval feeding is reminiscent of the provisioning condition in solitary bees, and lends itself to variation in size of female individuals. In these species the separation of worker and queen is not so obvious.

The basic principles of the change from worker to queen brood are doubtless the same in both groups of species, but nevertheless it is necessary to consider the change in the two groups separately. In all the species studied there is no external structural feature which separates worker from queen.

First it has been necessary to trace change in size of individuals throughout the season, and this has been done by taking nests of different sizes and stages of development, and analysing the brood and adults present. In this way it has been shown that in both groups of species the production of queens came as a sudden increase in average size, and not as a gradual increase, as has often previously been supposed, and is perhaps natural to suppose since the worker and queen appear to differ only in size.

Nests during the change-over from worker to queen brood were studied to find out how, during this change, brood was sorted out either into the queen or worker category. In the "pocket-making" species where individuals of approximately the same size may be either worker or queen, these were separated on a biometric basis which took into account their physiological make-up (*B. agrorum*).

It was thus apparent that in both groups of species some factor (or factors) was responsible for a sudden change in larval nutrition. The study of nests at the change-over (*B. agrorum*) indicates that only one type of female-producing egg exists. This is in keeping with the existing belief that the difference between queen and worker is one of quantitative larval nutrition, and therefore correlated with a state of economy in the nest.

The size of nests in the one species which produce queens varies very considerably, so that it seems that we may distinguish between the factors governing whether or not queens shall be produced, and factors governing the number of queens produced. The factors of the first category are the ones which most concern us. The type of season may govern the relative sizes of nests and the numbers of queens produced, but even in the worst seasons some queens are produced, and once a colony has been established for a certain length of time, it regulates its economy to queen production.

The first and most obvious factor to consider is the brood/worker ratio. It has been found that the larva/worker ratio must approach or fall below 1 before queen brood is produced. This immediately suggests that an egg-laying cycle could, through a fall in oviposition rate, effect a change in brood/worker ratio, with the subsequent production of queen brood, although on the surface such a mechanism might not appear able to produce the distinction between worker and queen which, though sometimes not obvious, does exist.

A study of the oviposition cycle showed a curve such as would produce the required brood/worker ratios, but it was obvious that about twice as many eggs were laid as produce brood, so that a change in the brood/worker ratio seemed to be independent of the oviposition rate of the queen. One is thus forced to believe that there is, during the greater part of the life of the colony, a considerable surplus of eggs, and that the destruction of these by workers controls brood/worker ratios. This destruction of eggs has been observed by several writers, and is also known to occur in ants and social wasps.

It is perhaps rather strange that this surplus of eggs should be found in nests when it is apparent that a measure of destruction is going on and the viable numbers are considerably fewer. We know that egg-eating does occur, so that the destruction of larvae instead of eggs does not provide a plausible explanation. It may be that maximum egg destruction occurs at night when the nest population is highest. The nests studied were for the most part taken during the afternoon. Although attention has not been drawn to this egg destruction mainly during the hours of darkness, records of Sladen (1912 : 244–251) show that this is so. From the data one can only assume that regulation of oviposition by the destruction of eggs takes place mainly during the hours of darkness, when the majority of the workers are in the nest. Pardi (1942) has shown that newly laid eggs are more liable to destruction in nests of *Polistes*, and this would also appear (Sladen, 1912) to be true in *Bombus*.

It has been shown that the premature death of the original queen will produce new queens a month earlier than is normal. The resulting change in brood/worker ratio is suggested as an explanation for this.

It seems probable that queen production in the normal nest is brought about by a reduction in the brood/worker ratio as a result of an increase in the destruction of eggs by workers. Why the workers should suddenly increase their destruction of eggs is not known, and it can only be suggested that their behaviour is altered by the production of male-producing haploid eggs by the original queen. In normal queen-producing nests invariably male brood is being, or has been produced. In the absence of other information, this explanation must seem to hold at least in the case of *B. agrorum*.

But such an explanation would not, on the surface, seem sufficient because of the clear-cut physiological differences between worker and queen in the one nest. The following facts and suggestions may help to explain a discontinuity which would not seem possible on the grounds of a change in the brood/worker ratio.

In the "pocket-making" species, queens, males, and workers may be produced in the one larval group. Where such is the case, the queens occupy the more central positions (see section on Larval Nutrition, etc.), so that females produced here fall into two categories. This does not exclude the production, at the change-over, of a few doubtful individuals, but it reduces their numbers. When these doubtful individuals emerge as adults there are clearly two alternatives—one to forage, the other to stay in the nest to feed and develop the fat-bodies of a queen. Which the individual may do may depend upon its individuality—for clearly the bees have individuality, as shown by the fact that in a nest that has lost its original queen, a limited number, independent of the size factor, develop ovaries—or on the amount of reserve material in the nest.

In the "pollen-storers" doubtful individuals very rarely occur. It is thought that in these species there is a sudden change to all or almost all male brood when the eggs giving rise to the sexual forms are laid, so that a return to female brood occurs at a higher level of economy in the colony.

These are the factors which tend to separate worker from queen once the brood/worker ratio has been reduced to that state where queen production is possible. Other factors, such as the division of labour, rise in nest temperature, availability of nectar and pollen, change from worker to male brood, are thought to be secondary factor influencing the amount rather than initiating the production of queen brood.

6. SUMMARY.

(1) Some features from the general biology of humble-bees which have a bearing on the problem of queen and worker differentiation have been discussed. These refer to development of ovaries in " spring " queens, temperatures in nests, larval nutrition and parasites.

(2) Larval nutrition has been studied to find out possible factors responsible for variation in size of worker individuals, and it has been shown how, in the " pocket-making " species, the more primitive method of larval nutrition which approaches the mass-provisioning condition provides greater opportunity, through larval relation with the food mass, for variation in size of adult individuals.

(3) Nests have been studied to determine the nature of seasonal population changes, and it has been shown that there is *not* a gradual increase in the average size of workers as the season progresses. In *B. agrorum* it appears more probable that there is a slight decrease in the average size up till the time of queen production.

(4) A division of labour into smaller " nurse-bees " and larger " foragers " is shown to be a significant phenomenon in several species, and it is shown that in some species there is a further division of " foragers " into individuals visiting flowers with deep nectaries and those visiting flowers with shallower nectaries.

(5) The development of ovaries in workers has been studied, and a method for numerical estimation of ovarial development has been described. The greatest stimulation to ovarial development is produced by the removal of the original queen. In her presence egg-laying by workers is confined to the period of production of the sexual forms, at which time the " pollen-storing " species are the more liable to develop laying workers.

(6) There are no structural differences between queen and worker, although some colour differences have been noted. Generally the queen is larger than the worker, her fat-bodies are markedly different, she is usually produced late in the season and she is fertilized, during which she may receive copulation marks which persist throughout life. The queen alone is able to hibernate and survive the winter.

(7) In the humble-bees belonging to the " pollen-storing " division there is almost always a marked gap in size between queen and worker, but this may not be well marked in the " pocket-making " division. Here it is necessary in dividing queen from worker to use some measure which takes into consideration the physiological make-up. This may be done satisfactorily by determination of weight/wing-length ratios.

(8) The brood of nests at the change-over from worker to male and queen production has been described. In the " pocket-making " species successive brood groups remain distinct, but this does not occur in the " pollen-storing "

species. In the former the sex and weight of pupae, prepupae and larvae of successive brood groups show that there is association of male and female brood in the same group (*B. agrorum*) and that females of two sizes may be present in the one group, but under these latter conditions the larger queen individuals usually occupy the central position. In *B. agrorum* the change-over is a gradual one, whereas that in the "pollen-storing" species appears to be more sudden.

(9) The brood/worker ratio in nests of different sizes has been studied, and it has been found that this must approach or fall below one before queen brood is produced.

(10) The study of numbers of eggs and brood found in nests, and the calculation of the viable egg-laying rate of the queen for nests at different stages of development, has shown that approximately half the eggs laid develop into adults. It would appear that this destruction of eggs by workers occurs mainly during the hours of darkness, for nests taken late in the day usually have the surplus of eggs.

(11) Egg destruction by workers is thought to be the main factor responsible for a reduction of the brood/worker ratio to that point where queen production is possible. Other factors such as change to male brood, increase in nest temperature, availability of nectar and pollen, and division of labour, are thought to govern more the amount of queen brood produced rather than initiating queen production.

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CONTENTS

PAGE
ROEPKE, W., Ph.D. The genus *Nyctemera* Hübner . . . . 47–70, 2 plates, 14 figs.

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THE GENUS *NYCTEMERA* HÜBNER.*

By W. Roepke, Ph.D.
(*Wageningen, Holland*).

Manuscript received 9th April, 1948.

(Read 1st September, 1948.)

With 2 plates and 14 text-figures.

A. THE SPECIES KNOWN FROM JAVA.

The genus *Nyctemera* was erected by Hübner in 1820 (*Verzeichniss*, etc. : 178), to include the following species : *hesperia* Cramer, *cafra* Drury, *nerina* Drury, *coleta* Cramer, *famula* Cramer, *atralba* Hübner (= *tripunctaria* L.) and *lacticinia* Cramer. From these, *lacticinia* was selected as the *typus generis* by Hampson (1894 : 46). Immediately after *Nyctemera*, Hübner placed his monobasic genus *Deilemera*, with *evergista* Cramer as sole species and, therefore, the *typus generis*. If one wishes to retain the name *Deilemera*, it can only be for *evergista* and its nearest allies, which are characterized, in the male sex, by the distinctly arched inner margin of the fore wing and the anal fold in the hind wing. As it is not yet possible to split up the genus *Nyctemera* into subgenera or even genera correctly, we treat *Deilemera* here as a synonym. Other synonyms are (alphabetically) :

Agagles White, 1841 : 482 (type : *amicus* White).
Atasca Swinhoe, 1892 : 139 (type : *pellex* L.).
Leptosoma Boisduval, 1832 : 197 (type : *annulatum* Boisduval (praeocc. !)).
Pitasila Moore, 1877 : 599 (type : *leucospilota* Moore).
Trypheromera Butler, 1881 : 45 (type : *plagifera* Walker).
Zonosoma Butler, 1881 : 44 (type : *cenis* Cramer (praeocc. !)).

Misspellings or modifications are : *Nïchtemera* Mabille, *Nychthemera* Mabille, *Nycthemera* Pagenstecher, Moore, *Nyctememera* Pagenstecher, *Nyctemeria* Matsumura, *Aglages* Kirby, *Dilemera* Hampson, *Leptosomum* Blanchard, *Tripheromera* Swinhoe. It is not advisable to make use of these names even if the old genus *Nyctemera* should be split up.

The systematic rank and position of the genus, within the large family (or superfamily) Lithosiidae (Arctiidae auct.) are not quite clear, but since Swinhoe (1895 : 18) most authors agree that it constitutes a separate subfamily, Nyctemerinae. Seitz (1910 : 102) even includes the common European Cinnabar moth, *Callimorpha jacobaeae* L. in it, and possibly this opinion may prove to be correct, as the caterpillar of this moth, by its general appearance and by its food-plant (*Senecio*), proves to be related to *Nyctemera*. The name *Callimorpha* Latreille, 1809, being older than *Nyctemera* Hübner, 1820, it is not unlikely that NYCTEMERINAE may become replaced by CALLIMORPHINAE in future. Meyrick (1885), Rothschild (1920), and more recently Tams (1935), however, include *Nyctemera* in the ASOTINAE (HYPSINAE auct.) without giving reasons. I cannot decide whether this is correct, but it seems to me somewhat doubtful.

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* The slides, manuscript, original drawings, photographs, negatives, etc., suffered badly during the war, and were partially destroyed. Fortunately, the manuscript could be replaced, but the drawings could only be replaced by rough sketches.—*Author.*

In the past several authors have devoted rather comprehensive attention to this genus; we mention Snellen van Vollenhoven (1863), Pagenstecher (1901), and Swinhoe (1903). Seitz (1915) reviewed the Indo-Australian species, and Bryk (1937) catalogued the species of the world. Pagenstecher (*l.c.*) gave a good historical sketch of the genus which he called emphatically " a history of errors."

The genus is represented by a fairly large number of species in the Indo-Australian region, extending to the Philippines, New Zealand and the Oceanic Islands. In Africa the number of species is restricted.

The moths are day-flying, somewhat mimicking certain Pierids, but they are also attracted by lamp-light. Though they are not rare in many localities, astonishingly little is known about their life-history. Horsfield and Moore (1858–59), figure the larva and pupa of what they call *lacticinia*, from Java, but which is certainly another species. They state that the larva " feeds on *Cacalia conchifolia*, which bears the native name of Tempo-wijung "—probably the same plant now known as *Senecio sonchifolium*. Some details of the Ceylonese *lacticinia* and *coleta nigrovenosa* are given by Moore (1882). Hudson (1898 : 2) records the common New Zealand *N. annulata* from several *Senecio* species and from *Cineraria maritima*, giving a brief description of the caterpillar. Recently Buxton, in Tams (1935*a* : 193) described the morphology of the *Deilemera alba* caterpillar from Samoa, unfortunately without adequate details concerning the life-history. He only says that it lives on a small composite weed "which grew in gardens, and was frequently a food-plant of this species."

It is a strange fact that females preponderate largely in collections, so that there may be some shortage of males for anatomical examination. The monotonous black and white pattern makes these insects rather unattractive to most collectors in the tropics, though extensive collecting may still reveal many interesting facts. The morphology of the entire group will not be treated here at length, as several authors, e.g. Kirby (1897), Hudson (1898), Hampson (1904), Swinhoe (1903) and Seitz (1915) have contributed in this direction. Only the male genitalia are described here for the first time, and are used on a large scale in order to arrive at a better understanding of the species under consideration. Furthermore, the tympanic organs may be briefly mentioned, though they are of little taxonomic value. They form two large cavities at the very base of the abdomen, with some structural relations to the metathorax. They are somewhat dislocated dorsally; in most species, chiefly in the males, they can be seen from above, as two lateral bladders. In some other species they are smaller and less obvious (cf. Saalmüller, 1884).

In spite of a large amount of literature, there exists a formidable confusion about the systematics and the nomenclature, even of some common species. The reason is the very simple pattern, which does not always exhibit striking differences and which is even liable to a considerable variability. The black coloration, for instance, may be extended at the expense of the white, or the reverse may be the case. Thus, the same species may appear in a dark or in a light coloured form, with all intergrades. Besides this, in certain species a general fading of the dark elements may occur; they may become very pale, but the typical pattern may be maintained. This variability may be due to certain genetic factors, and may therefore prevail in local populations or subspecies; in some other cases, however, it may be of an artificial origin, being caused by atmospheric conditions, such as rain, wind, sunshine, in connection with longevity of these day-flying moths.

In the course of years I examined a number of *Nyctemera* from different parts of the Malayan Archipelago; they can be easily distinguished by the male genitalia. The following is an attempt to revise the species known from Java. I have to thank the authorities of the Leiden and Amsterdam Museums for giving me full access to their collections. The material of the Leiden Museum deserves special attention, comprising the types of Snellen van Vollenhoven, Snellen and van Eecke. Furthermore, I had the privilege of looking through the collections of the British Museum, at South Kensington and Tring, and of the Hope Department, Oxford, and I beg to express my best thanks for the valuable assistance given to me.

The name *Nyctemera* is treated here as an anagram; this means that an adjectival species-name may be of any gender. I think it advisable, however, to follow Hübner, who treated it as feminine.

The following names are synonyms or are not NYCTEMERINAE at all.

1. *Nyctemera arcuata* Vollenhoven. This insect belongs to the CHALCOSIINAE, and is generally known as *Pseudonyctemera marginalis* Vollenhoven; see Snellen (1908 : 26), and Piepers and Snellen (1902 : 210).
2. *Nyctemera assimilis* Vollenhoven, see *N. tripunctaria* L.
3. *Nyctemera confusa* Swinhoe, see *N. tripunctaria* L.
4. *Nyctemera dentifascia* Kalis, nec Snellen, see *N. arctata* Walker.
5. *Nyctemera inconstans* Vollenhoven, see *N. latistriga* Walker.
6. *Nyctemera kondekum* Swinhoe, see *N. tripunctaria* L.
7. *Nyctemera inconstans* Vollenhoven, see *N. latistriga* Walker.
8. *Nyctemera leucostigma* Vollenhoven, see *N. latistriga* Walker.
9. *Nyctemera marginalis* Vollenhoven is a Chalcosiine, known as *Pseudonyctemera marginalis*; cf. *N. arcuata*.
10. *Nyctemera noviespunctata* Vollenhoven, see *N. maculata* Walker.
11. *Nyctemera nubecula* Vollenhoven, see *N. latistriga* Walker.
12. *Nyctemera pallens* Vollenhoven, see *N. latistriga* Walker.
13. *Nyctemera scalarium* Vollenhoven, see *N. arctata* Walker.

In the following list of the revised species they are arranged alphabetically, for reasons of convenience.

1. *Nyctemera arctata scalarium* Vollenhoven (fig. 1).

Walker, 1856 : 1664 ♂ : Cherra Ponjee. Vollenhoven, 1863 : 50 ♀ (*Leptosoma scalarium* de Haan i.l.) : Java. Walker, 1864 : 198 ♂♀ : Hindostan. Butler, 1888 ; 672. Swinhoe, 1892 : 147 (*Deilemera*). Hampson, 1894 : 45, fig. 21 ♂ (*Nyctemera*). Swinhoe, 1895 : 18 ♂♀ (*Deilemera*) : Shillong. Pagenstecher, 1898 : 199 (*maculata* nec Walker) : Lombok ; id., 1899 : 163. Swinhoe, 1903 : 64 (*Deilemera arctata*). Schultze, 1908 : 31 ♀, pl. 1, fig. 6 ♀ (*D. browni*) : Philippine Islands. Wileman, 1911 : 31 ♀ (*D. arctata albofasciata*) : Formosa ; id., 1915 : 111 ♂♀ (*D. luzonensis*) : Phil. Seitz, 1915 :

275, pl. 30 g, h (*D. arctata*). Reich, 1932 : 237 ♂♀, pl. 1, fig. 3 ♂, 7 ♀ (*D. arctata javana*) : Java ; id., ibid. : 238 (subsp. *kinabaluensis*) : Born. Kalis, 1934 : 14, figs. ♂♀ (*N. dentifascia* nec Snellen) : Java. Bryk, 1937 : 88 (*Deilemera*). Roepke, 1948 : 212 : Sum.

The species occurs only in the mountains of Java, chiefly at 1700–1800 m., where it is not rare at lamplight. It has a wide range, from N. India through Assam, Burma, Sumatra, Java, Borneo, Lombok, Philippines and Formosa. From the latter two localities subspecies are described. It is doubtful whether the specimens from various other localities should be considered as subspecies or not.

The nomenclature of the insect is rather confused, but easily settled. The topotypical *arctata* comes from the Eastern Himalaya slopes. The Javanese form was described by Snellen van Vollenhoven as *scalarium* de Haan i.1., and later on again by Reich as subsp. *javana*, whereas Pagenstecher confused it with *maculata* Walker and Kalis with *dentifascia* Snellen. I think the Javanese insect might represent a subspecies ; the name *arctata scalarium* Vollenhoven should be adopted. The type specimen of Vollenhoven is a female, in a rather damaged condition. It bears the label " Java " only.

The species is quite characteristic, so that it can hardly be confused with others. It is of a rather weak structure, the wings a little hyaline, the markings somewhat resembling a Geometrid of the genus *Abraxas*. These markings consist of a system of light greyish dots between the veins of the fore wing, more numerous and confluent in the male, less numerous, isolated or reduced in the female. The hind wing has only one row of marginal dots, confluent and forming a band in dark specimens, but more or less incomplete in light ones. These extremes with all intermediate stages give rise to a considerable variability, but nevertheless the species is easily recognizable at the first glance.

The male genitalia (fig. 1) have the uncus simply hook-shaped and bent downwards ; the aedeagus rather short and straight, with one chitinous tooth in its interior. This is the only occurrence of a spiculus in a Javanese *Nyctemera*. The valva is longer than broad ; at its upper basal angle it has a small, pointed appendage, directed inwards. The apex of the valva is deeply excised, so that two terminal lobes are formed, an upper one, shorter and more pointed, and a lower one, longer and more club shaped. Beneath the aedeagus there is a slender, juxta-like structure, elongate, with the apex bifurcate.

The weak structure of the insect, the peculiar markings, the neuration, the simple uncus and the spiculus in the aedeagus seem to justify the erection of a sub-genus, for which I propose the name **Arctata**. I see no reason to include the insect in *Deilemera*, as several authors have already done. Only the hind wing n_6 and n_7 are stalked as in *Deilemera*, but otherwise it differs from it in more than one respect. The neuration alone is not sufficient for placing it into *Deilemera*.

2. *Nyctemera baulus baulus* Boisduval (Pl. I, fig. 2 ♂ : text-fig. 2).

Boisduval, 1832 : 200 (*Leptosoma*) : Buru. Walker, 1856 : 1665 ♀ (*N. fasciata*) : Aneitum ; id., 1859 : 184 ♂♀ (*mundipicta*) : Singapore ; id., 1864 : 197 (*mundipicta*) ; id., ibid. : 198 (*simulatrix*) : S. Celebes ; id., 1866 : 1879 (*integra*) : Phil. Vollenhoven, 1863 : 43 (*L. baulus*) : Java. Kirsch, 1877 : 131 : New Guinea. Snellen, 1878–79 : 72. pl. 6, fig. 5 ♀ (*N. latistriga* nec Walker) : S. Celebes. Butler, 1879 : 162 : New Ireland ; Ternate. Snellen, 1880 : 34 (*L. latistriga*) : C. Sumatra. Pagenstecher, 1885 :

41 (*latistriga* nec Walker): Ceram; id., ibid.: 87: Aru; id., 1886: 120 (*latistriga* nec Walker): Aru Islands, Amboina, Nias, Sumatra. Meyrick, 1886: 15 (*tertiana*): Australia. Butler, 1887: 222 ♂♀ (*aluensis*): Solomon Islands. Druce, 1888: 573. Kirby, 1889: 167 (*L. integra*): Louisiade Islands; Phil.; Ternate. Snellen, 1889: 396 ♀: Roon Isl.; id., 1891: 252 ♂ (*latistriga* nec Walker): Flores. Röber, 1891: 352 (*latistriga* var. *fasciata*): Timor Laut; Goram; Maumeri; Ceram. Butler, 1892: 123 (*L. integra*): Phil. Swinhoe, 1892: 141, pl. 5, fig. 14 ♂ (*L. mundipicta*): Singapore; New Caledonia. Piepers & Snellen, 1896: 51 (*N. latistriga*): Talaut. Semper, 1899: 141, pl. 50, fig. 4 ♀ (*N. mundipicta*): Phil., etc. Holland, 1900: 560: Buru. Pagenstecher, 1900: 55 (*latistriga*): Bismarck Archip.; id., 1901: 118 (*baulus*); id., ibid.: 119 (*mundipicta*); id., ibid.: 120 (*integra*); id., ibid.: 120 (*latistriga*); id., ibid.: 121 (*picata*); id., ibid.: 121 (*aluensis*). Swinhoe, 1903: 75 (*Deilemera baulus* part.); id., ibid.: 74 (*simulatrix*); id., ibid.: 75 (*fasciata*); id., ibid.: 76 (*integra*); id., ibid.: 76 (*aluensis*); id., ibid.: 77 ♂♀, pl. 4, fig. 7 ♂ (*nisa*): Sangir. Turner, 1904: 471 (*N. baulus* part.). Pagenstecher, 1911: 435 (*latistriga*): Aru; Kei Islands. Seitz, 1915: 270 (*baulus*). Rothschild, 1920: 158 ♂♀ (*Deilemera mundipicta*): Sum. Van Eecke, 1927: 222; id., 1929: 349 (*N. baulus buruana*, nec *bouruana* Swinhoe): Buru; id., 1930: 209 ♂♀ (*baulus*): Sum.; id., 1932: 5 ♀: Riouw. Tams, 1935: 196 ♂♀, pl. 12, fig. 4 ♀ (*Deilemera mundipicta samoensis*): Samoa. Bryk, 1937: 54 (*Nyctemera baulus*, etc.).

It remains quite uncertain which species Boisduval (*l.c.*) described as *baulus* from Buru. By the kind assistance of Dr. Busnel, of Paris, I had a letter from the Muséum national d'Histoire naturelle, dated 25 février, 1943, informing me that Boisduval's type-specimen could not be traced there and must, therefore, be considered lost. For this reason it is advisable to consider the name *baulus* Boisduval definitely as an emendation of the species concerned, and to drop *mundipicta* Walker, as already used by several authors (Swinhoe, Rothschild, Tams), as a mere synonym, otherwise the name *baulus* will continue to cause confusion.

N. baulus is a fairly common species in Java. It is medium sized to rather large, and easily recognizable by the black marginal band in the hind wing, which forms a distinct tooth on n_2, directed inwards. The intensity of the greyish ground-colour in the fore wing is somewhat variable; in some specimens the transverse band shows a slightly yellowish tinge. The species bears a certain resemblance to *N. herklotsii*, the only one likely to be confused with it.

The male genitalia (fig. 2), which I was able to examine in several specimens from various localities (Sumatra, Java, Banggai, Buru), display a great uniformity. The uncus is dilated and rather loosely attached to the tegumen. The valva is broad and ends in two sharp processes, strongly bent towards each other, like a pair of forceps. The aedeagus is long and curved.

The species is distributed from Malaya to the Philippines, N. Australia and the Oceanic islands.

A number of subspecies have been described and may be distinguished virtually, though they cannot yet always be traced clearly in the Archipelago as the differences are mostly slight. I was able to examine the male genitalia of Van Eecke's *baulus buruana*, from Buru (= *baulus baulus* Boisduval), and they agree largely with those of several specimens from Java. From Sumatra a *Secusio picatus* Butler (1881: 380) has been described, which is generally included under *baulus* or *mundipicta*; it is, however, as already stated by Rothschild (1920), quite a distinct species. Swinhoe (1903: 81) states that *picatus* is "much like *regularis*." This is correct. *N. pagenstecheri*, from Lombok, listed by Bryk (1937) as a subspecies of *baulus*, is also doubtful.

Judging from Pagenstecher's and Seitz's figures, it may be a very light coloured *baulus*; the Leiden Museum has such pale specimens from Lombok and Flores that they may represent the true *pagenstecheri*. Unfortunately, there is another specimen in this collection, from Lombok, bearing a Fruhstorfer locality label and indicated as *pagenstecheri*. This is certainly another insect, as indicated by its dark coloration, with the transverse band broadly enlarged, forming a large, oval patch.

3. *Nyctemera coleta coleta* Stoll-Cr. (Pl. 1, fig. I ♂; text-fig. 3).

Cramer, 1782 : 153 ♂♀, pl. 368 H ♀ (*Phalaena Geometra*): sine patria. Hübner, 1820 : 178 (*Nyctemera*). Walker, 1854 : 399 : Ceylon; id., 1856 : 1663 (*colita* !): Ceram. Horsfield-Moore, 1859 : 322 ♂♀ (*coleta*): Java. Walker, 1861 : 93 : Born. Vollenhoven, 1863 : 39 (*Leptosoma*): Java, Mol. Snellen, 1877 : 5 : Java. Oberthür, 1878 : 469 (*Leptosoma*): Dorei, New Guinea. Moore, 1879 : 394 (*N. nigrovenosa*): Ceylon; id., 1882 : 48, pl. 98, fig. 4 ♀, 4*a* (larva, pupa). Butler, 1883 : 161 (*melaneura*): Nias. Pagenstecher, 1885 : 19 : Nias. Weymer, 1885 : 274 : Nias. Pagenstecher, 1886 : 122 : Aru. Moore, 1886 : 97 (*Nycthemera* !): Tavoy. Haase, 1886 : 523. Pagenstecher, 1888 : 114 : Amb.; id., 1890 : 101 (*Nycthemera* !): E. Java. Swinhoe, 1890 : 178. Snellen, 1890 : 221 : Sum. Röber, 1891 : 326 (var. *melas*): Ceram, Bankei. Swinhoe, 1892 : 140 (*coleta*). Hampson, 1893 : 12; id., 1894 : 49. Snellen; 1895 : 141 : Sum. Pagenstecher, 1895 : 114 : Buitenzorg; id., 1897 : 440 : Celebes; id., 1898 : 196 : Sumba. Semper, 1899 : 495 : Philippine Islands. Pagenstecher, 1901 : 142. Swinhoe, 1903 : 64 (*Deilemera*); id., ibid. : 64 (*nigrovenosa*); ib., ibid. : 65 (*melaneura*): id., 1903*a* : 67 ♂♀ (*coleta*): Malay Penins. Strand, 1910 : 200 ♀: C. Sum. Rothschild, 1915 : 215 ♂♀ : Ceram. Seitz, 1915 : 267, pl. 29*a* ♀ (*coleta*): id., ibid., ♀ (f. *subvitrea*). Rothschild, 1920 : 134 (*Deilemera*): Sum. Van Eecke, 1930 : 207. Roepke, 1935 : 4 ♀ : Sum. Tams, 1935 : 39 ♀ : Sum., Java. Bryk, 1937 : 59.

This species is the commonest *Nyctemera* in Java, flying everywhere, at daytime, from the coastal region up to an altitude of 1600 m. or more. It has a wide range, occurring in Ceylon, and from Assam through Malaya, the Archipelago, reaching the Philippines, N. Guinea and the Oceanic islands. In spite of this wide distribution it is less liable to variation, so that only a few subspecies have been recorded. These are characterized by an enlargement of the dark markings, as in *nigrovenosa* Moore from Ceylon, *melaneura* Butler from Nias, and *melas* Röber from Ceram and Bankei.

I have a number of specimens from various localities in Celebes (Bantimurang, Malino, Neengo, Todjambu) which have the dark markings more or less enlarged; possibly they belong to *melas* Röber.

The topotypical locality of the species is not known. In Java and Sumatra the species is remarkably uniform. Seitz (*l.c.*), however, records and figures a form *subvitrea*, which has the dark markings paler and somewhat reduced, the marginal band in the hind wing narrower, the hind wing nearly hyaline. The exact locality of this " form " is not given. The only specimen which I received from Java under this name, with a large number of normal ones, proved to be only a faded specimen, probably due to atmospheric influences.

The life-history in Java is unknown, though the late Mr. Rosier, from Buitenzorg, sent me a series of bred specimens without further details. The Ceylonese *coleta nigrovenosa* Moore feeds on *Gynura* and other Compositae (cf. Moore, 1882).

Morphologically the species is characterized by the hair brush of the male fore tibia, the peculiar male genital apparatus and by the nearly serrate antennae of the female.

This perhaps may give reason to erect a new subgenus, for which I propose the name **Coleta**.

The male genitalia (fig. 3) have the uncus modified in a special manner. It consists of a basal and an apical part, the former being distinctly separated from the tegumen, triangularly shaped, whereas the distal part is beak-shaped, strongly directed downwards and attached to the basal part on its underside. It looks as if the basal part is much elongated, surpassing the virtual top considerably. I call it tectum. Dorsally the chitinization of the tegumen, in its centre, is weak and membranaceous. The aedeagus is rather long and straight, supported by a weak chitinization dorsally, which I call junctus. The valva is longer than broad, its upper margin truncate at apex, its lower one elongated into a strong hook which is slightly bent downwards.

4. **Nyctemera crameri crameri** nom. nov. pro *lacticinia* auct. nec Cramer (Pl. I, fig. 9 ♂, 10 ♀; text-fig. 4).

? Horsfield-Moore, 1859 : 321, pl. 14, fig. 10 (larva), 10*a* (pupa) (*lacticinia* nec Cramer) : Java. ? Walker, 1861 : 93 (id.). ? Pagenstecher, 1901 : 117 (id.). ? Seitz, 1915 : 270 (id.).

Considerable confusion exists in regard to this species. I suppose that several authors, as given above, have identified it with *lacticinia* Cramer (1770 : 47, pl. 128 E ♂ : Coromandel). The latter, however, occurs in Continental Asia only, as far as I know ; and judging from the figures, as given by Cramer (*l.c.*) himself, Moore (1882) and Seitz (1910), as well as from three females in the Leiden Museum, it is quite different.[1] Possibly it is also confused in the collections with *tripunctaria* L., chiefly with the smaller forms, described as *assimilis* Vollenhoven. A new name, therefore, becomes necessary, though perhaps some older names may be available : in the first place *petulca* Sparrman, 1769, and *atralba* Hübner, 1820. If it were desirable to restore *petulca*, I think, however, it can only be applied to *trita* (see under this species) ; and *atralba* Hübner is given by Hübner himself as a synonym of *tripunctaria*, so that it has no nomenclatorial value at all. Furthermore, we have to deal with *confusum* and *kondekum* Swinhoe (1892), but both belong to *tripunctaria* L., as I was able to verify in the British Museum and at Oxford.

N. crameri superficially bears a great resemblance to *tripunctaria* f. *assimile* Vollenhoven, but both can be distinguished by the shape of the marginal band in the hind wing. In *crameri* this band is less broad, it reaches the costa, becoming tapering, and not filling up the space above n_7. The white band in fore wing is fully developed in all my specimens. I have a series of 1 ♂ and 12 ♀♀, all from E. Java only (Mt. Mayang, Mt. Raung, Mt. Idjen).

Possibly Horsfield (*l.c.*) figured the larva and pupa of this species ; by examination of his material, in the British Museum, this point might be elucidated.[2]

The male genitalia (fig. 4) are simple, the uncus being strongly hook-shaped, at its under surface somewhat edged. The valva is broad at base, but tapers immediately into a long, digitiform projection which surpasses the uncus. At the upper angle of its base it bears a strong, chitinous projection, more or less directed inwards, towards the aedeagus. The latter is rather short and slightly bent.

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[1] Mr. Tams, of the British Museum, kindly made a balsam mount and a photomicrograph of the *lacticinia* ♂ genitalia. They are indeed very different from *crameri*.

[2] During my visit I was not able to trace the Horsfield *Nyctemera* with certainty in the British Museum.

5. *Nyctemera distincta distincta* Walker (nec Swinhoe, 1903 : 58 ♂♀ : Sanghir) Pl. I, figs. 12 ♂, 13, 14 ♀, 17, 18 ♀; text-fig. 5).

Walker, 1854 : 392 : Java. Horsfield-Moore, 1859 : 331 ♂♀ : Java. Vollenhoven 1863 : 38 ♂♀ (*Leptosoma anthracinum* De Haan i.l.) : Java. Swinhoe, 1892 : 145 (*L. distinctum*). Pagenstecher, 1894 : 31 (*Nyctemera*); id., 1901 : 107 (*N. anthracinum* De H.); id., ibid. : 108 ♂♀, pl. 2, fig. 1 ♂ (*distinctum*). Swinhoe, 1903 : 69 (*Deilemera* (*Tripheromera*) *distincta*). Seitz, 1915 : 268 (*N. assimilis distincta*). Van Eecke, 1927 : 221 (*N. anthracinum* = *distincta* Walker, nec *assimilis* Vollenhoven). Bryk, 1937 : 61.

This species is recorded from Java only, where it seems to be confined to the mountainous region, up to 2000 m. It is a very variable insect, which is easily confused with *popiya* Swinhoe and certain other species. There are specimens with the dark ground-colour deep black, as charcoal, whilst in others this coloration shows a darker reddish brown or even a somewhat coppery tinge. The transverse band may be well developed, straight and clear, or more or less reduced, sometimes almost absent. The typical *distincta* of Walker having this band rather reduced, the name *anthracinum* Vollenhoven may be used for the variety with the band plain. A typical ♂ of this form is figured by Pagenstecher (1901, *l.c.*), but he gives no precise locality. I have similar specimens from Mt. Idjen in E. Java; presumably they may occur in the Eastern part of the island. Here the deep black and pure white coloration is more clearly seen than in any other *Nyctemera* from Java, which makes them very obvious. In one specimen of this series the white band has a very faint yellowish tinge. In my specimens from C. and W. Java this band is more or less reduced or even wanting. The marginal band in the hind wing is moderately to very broad, but not broadly extending along costa or anal region; in the centre distinctly narrowed, its inner border, therefore, somewhat angled. The abdomen has the tergites entirely black, only their hind margins bordered with white. In this respect the figure in Seitz (*l.c.*) is evidently wrong. The opinion of this author that *distincta* as well as *popiya* belong to *assimilis* is erroneous, as already pointed out by Van Eecke; furthermore, *distincta* Walker has priority, and finally *assimilis* is not a distinct species.

The male genitalia (fig. 5) are of a peculiar structure, chiefly on account of the complicated uncus. The latter is rather small, and separated from the broad, triangular tegumen by a strong constriction. Its actual top is strongly directed downwards; dorsally it bears some bristles which are easily lost by maceration. Furthermore, the uncus has two latero-dorsal appendages which, seen from aside, are hook-shaped, whereas from above they have the shape of ear-like projections. The valva is elongated, narrow, about four times as long as broad and much surpassing the tegumen plus uncus; it may be called somewhat irregularly spoon-shaped, its apex being broadened asymmetrically and being dentate. The aedeagus is of medium length, slightly bent downwards and suspended in a bridge-like chitinous connection between the bases of both valvae. It may be considered as a combination of a junctus and a juxta, with a sharp circular aperture in its centre for the aedeagus.

6. *Nyctemera herklotsii herklotsii* Vollenhoven (Pl. I, fig. 3 ♀; text-fig. 6).

Vollenhoven, 1863 : 39 ♂ (*Leptosoma*) : Java; id., ibid. : 40 ♂ (*quadriguttatum*) : Java. Swinhoe, 1892 : 141 (*mundipicta* part., nec Walker). Pagenstecher, 1901 : 113, pl. 2, fig. 5 ♀ (*herklotsi* !); id., ibid. : 114, pl. 2, fig. 9 ♂ (*quadriguttatum*) : Java. Swinhoe, 1903 : 71 (*quadriguttatum*); id., ibid. : 75 (*baulus* part., nec Boisduval). Seitz, 1915 : 269, pl. 29 h ♀ (as *sexmaculata* ex err. !). Van Eecke, 1927 : 221. Bryk, 1937 : 63.

This species seems to be confined to Java only. It is a mountain insect, occurring at an altitude of 1500 m. or higher, where it is not common.

It resembles the common *baulus*, with which several authors have confused it. The general coloration is mostly denser black; the marginal band in the hind wing is broader. The transverse band in the fore wing often shows symptoms of reduction and then may be divided into several spots; such a form has been described by Vollenhoven as *quadriguttatum*. I have seen specimens in which only traces of this white band were present. The marginal band in hind wing shows the same tooth on n_2 as in *baulus*.

The male genitalia (fig. 6) are characterized by a pointed uncus which is nearly straight. The valva is rather broad, with the upper apex pointed and having below it a long, digitiform processus which gives a peculiar appearance to this organ. The lower margin of the valva is thickened. The aedeagus is of moderate length, its apical portion is strongly curved upwards. From the upper angle of valva base a chitinous communication runs which seems to support the aedeagus dorsally, and which I call junctus.

Swinhoe (1892 : 144) describes a *Deilemera kondekum* ♂♀ from Java which is considered by Pagenstecher, Seitz and Bryk as a synonym of *herklotsii*, though Swinhoe (1903 : 72) states positively that it has no affinity with this species, " being more nearly allied to *distincta* Walk." Professor Hale Carpenter sent me a photograph of Swinhoe's type-specimens. This enables me to settle this very doubtful question : *kondekum* belongs to what is treated here as *tripunctaria* L. (see p. 60).

Nyctemera instar Rothschild.

Rothschild, 1920 : 135 ♂♀ (*Deilemera*): Sumatra. Bryk, 1937 : 65 (*Nyctemera*): Java, Sumatra.

This species, described from Sumatra only, is recorded by Bryk from Java also, without further details. I have never seen any species from Java that might be identified with it, and I think that Bryk's statement is probably erroneous.

7. *Nyctemera latistriga latistriga* Walker (Pl. I, fig. 4 ♂ ; Pl. 2, fig. 3).

Walker, 1854 : 397 : Moulmein. Horsfield-Moore, 1859 : 331 ♂♀ : Java, Canara. Walker, 1861 : 93 : Born. Vollenhoven, 1863 : 44 ♂♀ (*Leptosoma leucostigma*) : Java ; id., ibid. : 45 ♂ (*pallens*) : Java ; id., ibid. : 47 (*inconstans*) : Java ; id., ibid. : 49♂ (*nubecula*) : Java. Snellen, 1880 : 34, pl. 3, fig. 11 ♂ (*L. inconstans*) : C. Sum. Butler, 1881*a* : 44, pl. 88, fig. 1 (*L. latistriga*) : Moulmein, Ceylon. Pagenstecher, 1884 : 214 (*N. latistriga*) : Amb., id., 1885 : 19 : Nias. Snellen, 1884–85 : 39 (*N. inconstans* = *latistriga* Butler !) : Cel. Weymer, 1885 : 274 : Nias. Pagenstecher, 1886 : 120 : Aru. Moore, 1886*a* : 54. Pagenstecher, 1887 : 113 : Amb. Swinhoe, 1890 : 178 ; id., 1892 : 142 (*Leptosoma*) : Moulmein, N. Born., Ceyl., Phil., Java. Hampson, 1894 : 47. Swinhoe, 1895 : 18 : Assam. Pagenstecher, 1897 : 439 (*inconstans*) : Born., id., ibid. : 440 : Uliasser ; id., 1898 : 196 (*lombokiana* Fruh.) : Lombok ; id., ibid. : 198 (*arcuata* neo Vollenhoven) : Lombok. Snellen, 1899 : 23. Semper, 1899 : 453, pl. 58, fig. 3 ♀ : Phil., etc. Pagenstecher, 1901 : 128. Swinhoe, 1903 : 78 (*Deilemera*). Swinhoe, 1904 : 82 ♂ (*N. ovada*) : Sumba. Strand, 1910 : 200 ♂ (*Deilemera*) : C. Sum. Seitz, 1915 : 267, pl. 29c ♂♀ (*Nyctemera*) ; id., ibid. : 268 (*trita leucostigma* ; *trita nubecula*). Rothschild, 1920 : 134 (*D. consobrina*, nec Hopff.) : Korintji. Van Eecke, 1927 : 222 ; id., 1930 : 210. Bryk, 1937 : 76 ; id., ibid. : 69 (*leucostigma*) ; id., ibid. : 72 (*pallens*) : Java.

This species has a wide range, from Continental Asia through the Archipelago, reaching the Moluccas and the Philippine Islands. I have not yet seen it from New Guinea and Australia. In Java it is apparently less common; I have only a small series from various localities in W. Java, but I am sure that it occurs everywhere.

Though very variable, it is easily recognizable by its general appearance, with the domination of the white colouring, chiefly produced by the broad basal streak in the fore wing. In the Javanese specimens the dark coloration is generally rather pale, showing a distinct tendency to fading. When the white markings are also extended very pale specimens may result, described as *pallens* by Vollenhoven. On the other hand, darkened specimens occur, though only very occasionally, in which the white fore-wing markings are nearly or completely extinct. Such specimens were described by Vollenhoven as *leucostigma* and *nubecula*, the former still showing an obsolete, white patch near the costa, the latter being uniformly dark, both with only a slight trace of a transversal shade. This darkening makes the insect practically unrecognizable; to all authors *leucostigma* and *nubecula*, therefore, remained a problem, and Seitz (1915) refers them to *trita*. This problem, however, was solved at once by an examination of the male genitalia in one of the *nubecula* paratypes of Vollenhoven. They show the *latistriga* character so convincingly that there cannot be the slightest doubt that *nubecula*, with *leucostigma* and *latistriga*, are the same. Moreover, the marginal band in the hind wing has the same shape, characterized by the prominent tooth on n_2. The British Museum has one quite typical male of *latistriga* f. *leucostigma* Vollenhoven, from Waingapo, as *ovada* Swinhoe; the latter name now falls as a synonym (see Pl. 2, figs. 3 and 7).

The nomenclature of the species, of course, now becomes rather complicated, and the synonymic lists, as published by several previous authors, are less reliable. Snellen constantly called the insect *inconstans*, erroneously referring *latistriga* to what we consider here as *baulus* Boisduval. The topotypical form came from Moulmein, Burma, according to Swinhoe; if the Javanese form proves to be a subspecies, one of the names given by Vollenhoven, becomes valid. *Leucostigma* has priority, followed by *pallens*, *inconstans* and *nubecula*. Of these, *inconstans* ought to be chosen, as the other names refer to very occasional aberrations only. *Pallens* may be applied to the palest varieties, *leucostigma* and *nubecula* to the darkest.

The male genitalia could only be examined in one specimen from Medan, Sumatra and in one of Vollenhoven's paratypes of *nubecula* from Java.[3] They are rather typical, and show the uncus strongly developed, bent downwards, and at its base dorsally with two prominent hooks. The valva ends in three pointed processes, the first of which is situated at its upper basal angle; it is the smallest one; its shape is rather dentiform. The second is the largest one, forming the virtual distal top of the valva; it is slightly bent downwards. The third is smaller, straight, situated beneath the second. Second and third processes together have the shape of an asymmetrical forceps. The aedeagus is very short, only very slightly bent upwards; it is surrounded by the same structure as in *herklotsii*, consisting of a junctus dorsally in combination with a juxta ventrally.

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[3] Slides and drawings lost; see footnote, p. 47.

8. *Nyctemera maculata maculata* Walker (Pl. I, fig. 24 ♂; text-fig. 12).

Walker, 1854 : 396 (sine patria). Vollenhoven, 1863 : 42 ♂♀ (*Leptosoma noviespunctatum*): Java. Pagenstecher, 1894 : 31 (*Nyctemera noviespunctata*); id., 1901 : 168, pl. 2, fig. 10 ♂ (*Deilemera maculata*): Lombok, Java. Swinhoe, 1903 : 62. Seitz, 1915 : 275, pl. 30 f ♀ (species altera ?). Van Eecke, 1927 : 22. Bryk, 1937 : 90.

This species is known from Java only, but Pagenstecher records it also from Lombok. I have a small series from various localities in W. Java; presumably it is a rather rare insect. It is clearly distinguishable by the double white basal streak in fore wing; the hind wing has the costa pure white. In the male the posterior margin of the fore wing is curved, with the tornus rounded; the hind wing has the anal margin folded over, forming a distinct anal fold. The tympanic cavities in both sexes are less obvious. The figure given by Pagenstecher is typical; that of Seitz is not correct; it shows a specimen with the double basal streak in fore wing practically wanting (I have never seen such an aberration !), or it represents another subspecies or species.

The male genitalia (fig. 12) are of a more robust construction, the uncus is narrow, pointed and straight, the tegumen broad, distinctly separated from the uncus. At its inner base the tegumen has two hook-shaped appendages with the tops somewhat dentate. The valva is simply built; it bears a long terminal process which has the shape of a slender club. Near base of upper margin the valva has a smaller digitiform process. The aedeagus is rather stout and slightly curved.

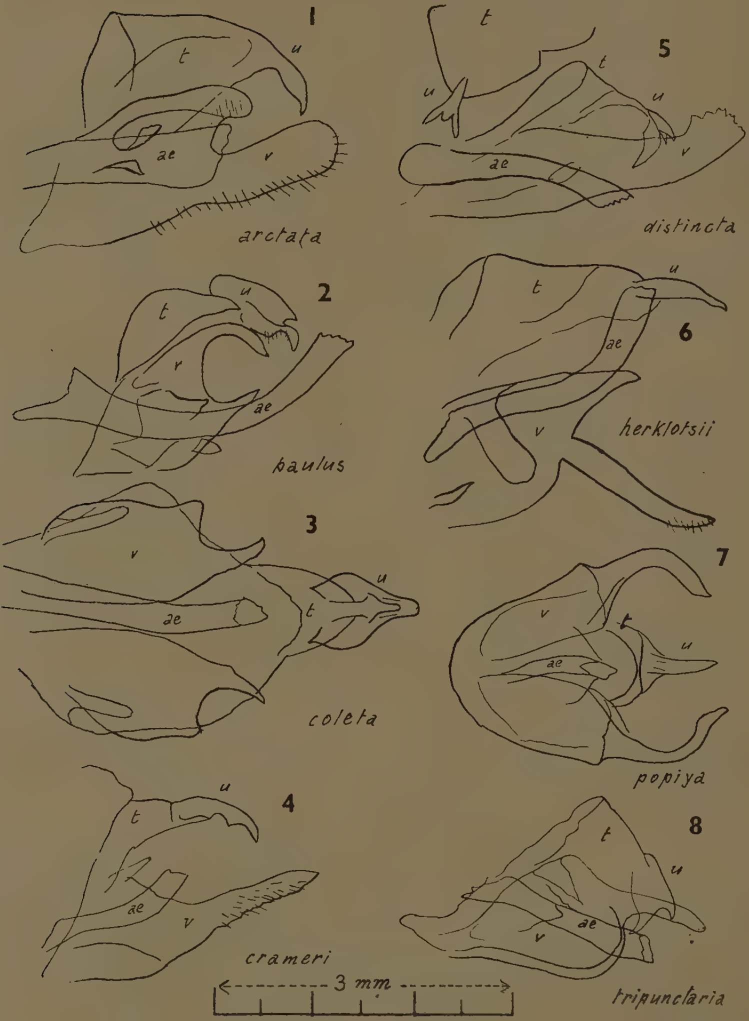
N. maculata Walker belongs to the same group as *evergista* Cramer, which is the type of Hübner's genus *Deilemera*. No doubt the general appearance, the shape of the fore wing and the anal fold in the hind wing of the male, the neuration in both sexes and the structure of the male genitalia justify the introduction of a separate genus, or at least of a subgenus, for which the name ***Deilemera*** Hübner exclusively should be used.

9. *Nyctemera popiya popiya* Swinhoe (Pl. I, fig. 11 ♀, 15, 16 ♂♂; text-fig. 7).

Swinhoe, 1903 : 69 ♂♀, pl. 3, fig. 3, 7 ♂ (upper- and underside) (*Deil.* subg. *Tripheromera*): Java. Seitz, 1915 : 268 (*assimilis popiya*), pl. 29e. Bryk, 1937 : 61 (*distincta* forma *popiya*).

This species is known from Java only. I have a small series from various localities in W. Java, lowland and lower mountains. It bears a strong resemblance to *N. distincta*, with which it is confused by Seitz and Bryk. It can be distinguished from *distincta*, however, at the first glance by the different shape of the marginal band in the hind wing. *Distincta* has it excavated in the centre; in *popiya* its inner border is regularly rounded, at anal angle mostly suddenly tapering. The ground-colour of fore wing is a dark reddish brown, the transverse band is wanting, as in Swinhoe's typical specimens, or represented by a slight trace. The basal part of the veins in fore wing is yellow; the patagia, tegulae and notum are fringed with dark yellow. Abdomen as in *distincta*.

The male genitalia (fig. 7) are very different from those of *distincta*, demonstrating that both species belong to different groups, though superficially they have the greatest resemblance. In the first place tegumen and uncus are simple, the former triangular,


1
t
u
ae
v
arctata
5
t
t
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u
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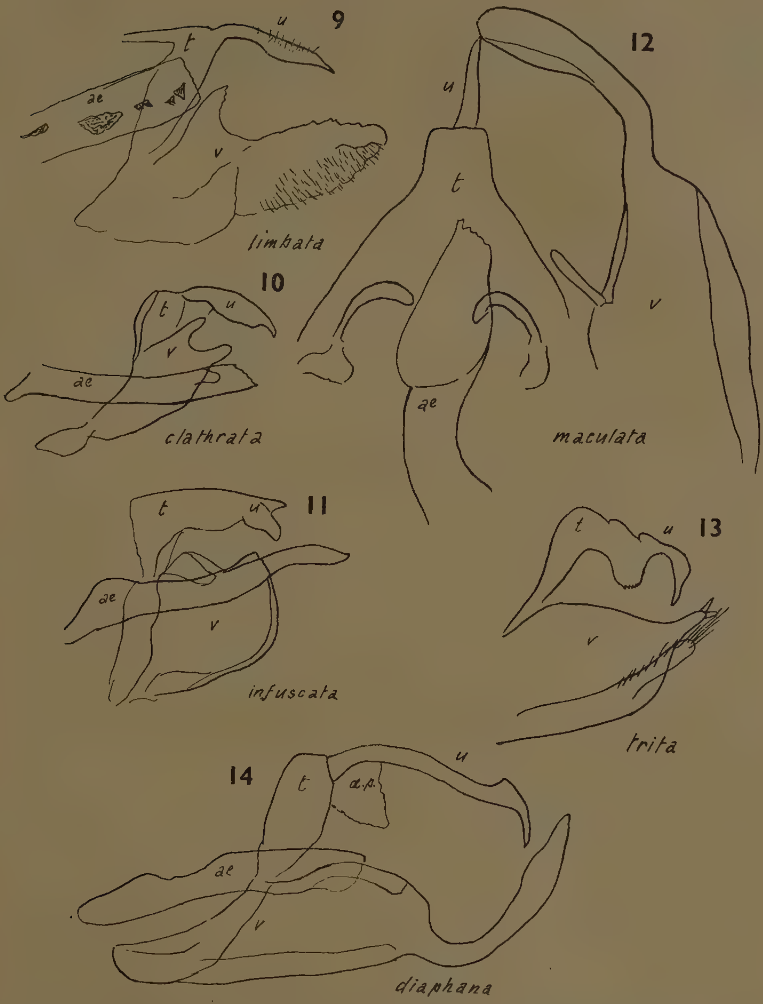
ae
distincta
2
t
u
r
ae
paulus
6
u
t
ae
v
herklotsii
3
v
u
t
ae
coleta
7
v
t
u
ae
popiya
4
u
t
ae
v
crameri
3 mm
8
t
u
ae
v
tripunctaria

FIGS. 1–8.—Male genitalia of *Nyctemera* Hübner. All sketches on the same scale. *ae*, aedeagus; *t*, tegumen; *u*, uncus; *v*, valva.


9
t
u
ae
v
limbata
10
t
u
v
ae
clathrata
11
t
u
ae
v
infuscata
12
u
t
ae
v
maculata
13
t
u
v
trita
14
t
a.p.
u
ae
v
diaphana

FIGS. 9–14.—Male genitalia of *Nyctemera* Hübner. For explanation see Figs. 1–8.

the latter narrow, slender, hook-shaped and bent downwards, a little edged at its undersurface. The separation between tegumen and uncus is distinct, as usual in this genus. The aedeagus is short and slender, slightly bent. The valva is obviously elongated into a long, terminal process, which may be called stag-like on account of its curved shape, being strongly bent inwards as well as slightly upwards. In one specimen from G. Tjisuru, W. Java, the top of this process is simple, though somewhat irregularly broadened; in another, from Pamegattan, near Garut, W. Java, it is distinctly bifurcate. Furthermore, there is a junctus and a narrow, faint, juxta-like structure supporting the aedeagus from above and from below. The valva has an interior appendage, like an auricula, broad and triangular, with its base reaching lower margin of valva.

10. *Nyctemera tenuifascia tenuifascia* Snellen (Pl. 2, fig. 1 ♂).

Snellen, 1898 : 26 ♂, pl. 1, fig. 2 ♂ : Lombok. Pagenstecher, 1898 : 198 ♂; id., 1901 : 123 ♂ : Lombok. Swinhoe, 1903 : 84 (*Deilemera*). Snellen, 1907 : 115 ♀ (*Nyctemera*) : Java. Seitz, 1915 : 271 ♂, pl. 29*i* ♂ : Lombok. Bryk, 1937 : 82 : Lombok.

The largest *Nyctemera* from Java, only known from the Tengger Mts., but I have a male from Mt. Lawu, C. Java (leg. Rosier). It must be a rare species, as I have only one male and one female from Tosari, Tengger, and I never received it among the large numbers of Heterocera which were sent me from this region by several collectors.

The insect is very conspicuous, and cannot be confused with other species. The fore-wing band is narrow in the male from Mt. Lawu, but broader in the male and the female from Mt. Tengger. In the latter specimen the thorax above is white, with some black dots, and only a little yellow chiefly along the hind margin of patagia. In the former the patagia, tegulae and the notum are mixed with yellow scales. The female antenna is nearly as bipectinate as in the male. The tympanic cavities, in both sexes, are much reduced in size.

There is only one female from Tosari, Tengger Mts., in the Leiden Museum, mentioned by Snellen (1907). His type-specimen, from Lombok, came from the Pagenstecher Collection, now at Munich. The figure of this specimen shows the transverse band in the fore wing much narrower than in the Javanese specimens; possibly the latter may prove to be a subspecies.

The male genitalia have not been examined microscopically, but as far as I can see in the one specimen from Tosari, without maceration, the uncus is pointed, directed downwards; the valva ends in a beak-like hook, with a thumb-like inner process near base of this hook.

11. *Nyctemera tripunctaria tripunctaria* L. (Pl. I, figs. 5, 6 ♂♂, 7, 8 ♀♀; text-fig. 8).

Linnaeus, 1758 : 523 (*Phalaena Geometra*) : Asia. Cramer, 1775 : 34, ♂♀, pl. 22 E ♂ : sine patria. Hübner, 1820 : 178 (*Nyctemera atralba*). Walker, 1854 : 397 (*tripunctaria*) : Penang; China; Assam; E. India. Horsfield-Moore, 1859 : 332, ♂♀ : Penang. Vollenhoven, 1863 : 39 (*Leptosoma tripunctarium*) : Java; Sum.; Born.; id., ibid. : 39 ♀ (*assimile*) : Java. Walker, 1864 : 199 ♂ (*celsa*) : Siam. Piepers and Snellen, 1877 : 5 (*N. tripunctaria*) : Batavia. Aur., 1882 : 163. Pagenstecher, 1885 : 18 (*assimile*) : Nias. Moore, 1886 : 97 (*Nycthemera* ! *tripunctaria*) : Tavoy. Pagenstecher, 1890 : 101 (*N. assimile*) : E. Java. Swinhoe, 1892 : 141 (*Leptosoma tripunctaria*) : Singapore; Malay Penins.; id., ibid. : 142 (*celsum*) : Cambodja; China; id., ibid. : 144 ♂♀ (*confusum*) : Java; id., ibid. : 144 ♂♀ (*kondekum* [p. 318 index : *kondecum* !]) : Java.

Hampson, 1894 : 47 (*N. tripunctaria*). Pagenstecher, 1898 : 198 (*assimile*) ; id., 1901 : 108, pl. 2, fig. 3 ♀ (*assimile*) : Java, Sumba ; id., ibid. : 118 ♂ (*celsa*) ; id., ibid. : 137 (*tripunctaria*) ; id., ibid. : 139, pl. 2, fig. 6 ♀ (*sumatrensis* nec Heyl.). Swinhoe, 1903 : 77 (*Deil. kondeka*) ; id., ibid. : 80 (*tripunctaria*) ; id., 1903*a* : 66 ♂♀ : Malay Penins. Strand, 1910 : 200 (*Nyctemera*) : C. Sum. Seitz, 1915 : 267 (*N. tripunctaria*, ab. *sumatrensis* Pagenstecher, *celsa* Walker, *candidissima* f. nov., *alba* Pagenstecher ?, *gratia* Schultze) ; id., ibid. : 268 (*assimile*) ; id., ibid., pl. 29*a* (*tripunctaria* ♂, *sumatrensis* ♀) ; id., ibid., pl. 29*b* (*celsa* ♂♀, *candidissima* ♀). Swinhoe, 1916 : 213 (*Deilemera tripunctaria* L. (nec auct.) = *annulatum* Boisduval (ex err. !)). Van Eecke, 1930 : 208 (*N. tripunctaria*) : Sum. Bryk, 1937 : 82 (*tripunctaria*) ; id., ibid. : 83 (f. *elzuniae-kruscheae*) : Sum. ; id., ibid. : 92.

The species is distributed from S. China and Assam through Siam and Malaya, Sumatra, Java, Borneo, and reaches Sumba (Pagenstecher). In Java it occurs everywhere, from about sea level (Depok) up to an altitude of about 1500 m. (Idjen Plains), and it is not rare. It displays an amazing variability, geographically as well as locally. This fact gives rise to a complicated synonymy which cannot easily be rectified with certainty. The existing confusion is largely augmented by Swinhoe (1916), who has shown that the specimen in the Thunberg collection at Upsala, which he claims to be the type-specimen of Linnaeus, belongs to what is known as *annulatum* Boisduval, from New Zealand. Without denying the correctness of this statement, it is evident, however, that Linné's diagnosis, " . . . anterioribus fascia interrupta baseosque stria ; posterioribus disco albis " never refers to *annulatum* Boisduval, so that there is only one conclusion, viz. that the Thunberg specimen is not the same as the type-specimen of Linnaeus. We have, therefore, to retain Linné's name for the species. Swinhoe, furthermore, places *petulca* Sparrman under the synonyms, but this question remains very doubtful (see under *trita*, p. 62).

In Java the insect is medium sized to rather large, though smaller specimens may occur occasionally, mainly in the mountains. The white band in the fore wing may be broad and plain or dissected by dark veins, or even more or less overshaded by the dark, greyish brown ground colour. The white basal streak may be fully developed, or may completely disappear by gradual reduction. Chiefly in smaller specimens of the *assimile* type, it is almost absent. The basal part of the venation, as a rule, is white. The hind wing has the marginal band generally broad, its inner border regularly rounded, sometimes a little crenulate or obtuse ; it extends broadly along the costa, filling up the space above n_7. The base of the hind wing is slightly greyish ; the same coloration also occurs along the anal margin. These markings in the hind wing may be much enlarged, so that in extreme cases only a white discal patch remains. Such a dark form is probably described by Swinhoe as *confusum*, though this needs confirmation by re-examination of the type-specimen in the Oxford Museum. Furthermore, Swinhoe (1892 : 144) described a *Leptosoma kondekum* ♂♀ from Java called *kondecum* in the index on p. 318 and *Deilemera kondeka* in 1903 : 77. This species, from the description only, remains a puzzle ; fortunately, I am indebted to Prof. Hale Carpenter for a photograph of the type-specimens. Both seem to be females, the one with the transverse band in fore-wing clear and broad, the other with this band rather darkened. This band is the same as in our *tripunctaria* and *assimilis* Voll. Unfortunately, the hind-wing costa is covered by the hind margin of the fore-wing in both specimens. From Swinhoe's diagnosis, however, we have to conclude that the costa in the hind-wing is darkened, therefore I am sure that the species belongs to *tripunctaria* L. The abdomen is white or light greyish, with a median row of darker dots on the tergites. Smaller specimens with the white basal streak in the fore wing wanting and the transverse band overclouded by the dark ground-colour were described by Vollenhoven as *assimile.* His type material consists of two female specimens only. Pagenstecher (1901) has figured this form correctly. There are, of course, all intergrades between *assimile* and *tripunctaria.* In Java such intermediate forms prevail.

The male genitalia of a typical *tripunctaria* from Java (fig. 8) and of *assimile* are so similar that they must be considered as one and the same species. The tegumen is broad, the uncus short, bent downwards; dorsally it has a short projection, which may be somewhat truncate in some specimens and more hook-shaped in others. The aedeagus is short and fairly straight; it is supported by a junctus. The valva is short, about as broad as long, its lower margin and rounded lower apical angle thickened, its upper angle elongated into a long digitiform process, the shape of which is somewhat variable in some specimens. The upper basal angle of the valva bears a strong appendage of a slender triangular shape, directed inwards or slightly downwards. I call it auricula.

12. *Nyctemera trita trita* Walker (Pl. I, figs. 20, 21 ♂♂, 22, 23 ♀♀; text-fig. 13).

Walker, 1854 : 394 : Java. Horsfield-Moore, 1859 : 331 ♂♀, pl. 8*a*, fig. 9 ♂ : Java. Pagenstecher, 1890 : 197 (*Nycthemera* !). Swinhoe, 1892 : 143 (*Leptosoma tritum*). Pagenstecher, 1901 : 109 (*Nyctemera trita*). Swinhoe, 1903 : 69 (*Deilemera* (*Triphero-mera*)). Seitz, 1915 : 268, pl. 29*d* ♂ (upper side), 29*e* (under side) (*N. tritum* !). Bryk, 1937 : 82.

This species, small to medium sized, is only recorded from Java, where it is not rare, occurring at sea level as well as in the mountains (Idjen Plains).

The ground-colour is a greyish brown; the fore-wing band is well developed and rather broad or reduced to a weak trace. In the hind wing the dark margin is mostly broad, but not extending along costa broadly. The base of hind wing and anal margin, mostly up to n_2, are more or less suffused with dark, so that in many specimens the white coloration is reduced to a discal patch of variable dimensions. In the darkest specimens it may be nearly absent. The darkening of the hind wing does not always correspond with that of the fore wing; there are specimens with dark hind wings and a well-developed band in the fore wing, as well as others with the fore wings darkened and the hind wings rather white.

The abdomen is of a light greyish or nearly white coloration, with a dorsal row of dark patches near anterior border of each tergite. The name of the species may be a little doubtful, since Sparrman (1769 : 500) described a *Phalaena petulca* as " aliis fuscis . . . inferioribus disco albis." As a habitat he gives " Neuw Baij," at a distance of two days' sailing from Java. If Sparrman's type-specimen still exists, this question could easily be settled by re-examination; otherwise the name *petulca* should be suppressed in order to avoid continual confusion. Or, if emendation is desirable, it should replace *trita* only.

The male genitalia (fig. 13) are of a peculiar construction. The uncus, strongly directed downwards, is sharply separated from the tegumen. The latter is broadly dilated into two lateral lobes, their margins being covered with distinct spines. The aedeagus is rather long and slightly bent upwards, with the apex broadened. The valva is a little longer than broad; it is terminated by a bifurcate process, somewhat curved inwards. Furthermore, the valva has a harpe-like appendage near its inner and lower margin, rather long and blunt, which at its very top bears a bundle of long, stiff bristles. The aedeagus is of medium length, slender, very slightly bent upwards. It is supported by a junctus somewhat projecting forwards.

Briefly summarizing the results obtained by the foregoing investigation, we arrive at the following arrangement of the *Nyctemera* species known from Java (alphabetically):

PAGE

1. *N.* (subgen. *Arctata* Roepke) *arctata scalarium* Vollenhoven 49
   Synonyms:
      maculata Pagenstecher (nec Walker).
      arctata javana Reich.
      dentifascia Kalis (nec Snellen).
2. *N. baulus baulus* Boisduval 50
   Synonyms:
      mundipicta Walker.
      simulatrix Walker.
      latistriga Snellen (nec Walker).
      baulus buruana van Eecke.
3. *N.* (subgen. *Coleta* Roepke) *Coleta coleta* Cramer 52
4. *N. crameri crameri* Roepke 53
   Synonym:
      lacticinia auct. (nec Cramer).
5. *N. distincta distincta* Walker 54
   Synonyms:
      anthracina Vollenhoven.
      assimilis Seitz (nec Vollenhoven).
6. *N. herklotsii herklotsii* Vollenhoven 54
   Synonyms:
      quadriguttata Vollenhoven.
      mundipicta Swinhoe (nec Walker).
      sexmaculata Seitz.
7. *N. latistriga latistriga* Walker 55
   Synonyms:
      leucostigma Vollenhoven.
      pallens Vollenhoven.
      inconstans Vollenhoven.
      arcuata Pagenstecher (nec Vollenhoven).
      ovada Swinhoe.
      trita leucostigma Seitz.
      trita nubecula Seitz.
      consobrina Rothschild (nec Hopffer).
8. *N. maculata maculata* Walker 57
   Synonym:
      noviespunctata Vollenhoven.
9. *N. popiya popiya* Swinhoe 57
   Synonyms:
      assimilis popiya Seitz.
      distincta f. *popiya* Bryk.
10. *N. tenuifascia tenuifascia* Snellen 60

PAGE

11. *N. tripunctaria tripunctaria* L. 60
    Synonyms :
        ? *atralba* Hübner.
        assimilis Vollenhoven.
        confusa Swinhoe.
        kondekum Swinhoe.
        sumatrensis Pagenstecher (nec Heyl.).
        annulatum Swinhoe (nec Bsduval.).
12. *N. trita trita* Walker 62

P.S.—In the British Museum I saw an old female specimen of *N. amplificata* Walker labelled Java, without further indication. It is a small species, entirely white, without any trace of dark markings on the wings. It is only known from Nias, and therefore the habitat "Java" is not unlikely to be wrong.

B. SOME NEW OR LITTLE-KNOWN MALAYAN SPECIES.

Having examined the male genitalia of a number of Malayan species of *Nyctemera*, it seems to me desirable to put on record some of the results. These are frequently of the greatest importance in the separation and correct identification of the species, and therefore authors should, in future, give particular attention to this point. It is probable that a correct arrangement of the many species in subgenera would prove to be possible on this basis.

1. **Nyctemera diaphana** sp. n. (Pl. 2, fig. 6, text-fig. 14).

♂♀. Wings rather thinly scaled and therefore slightly hyaline.

♂. Fore wing light greyish brown, with a broad, transverse band reaching from 2/3 costa to inner margin, near tornus. This band is somewhat broadened in the middle, with its inner and outer border distinctly dentate, thus forming pointed projections on the veins. A basal streak, somewhat obtuse, is present. Hind wing with the apex slightly projecting, with the costa somewhat darkened, the outer margin with a rather regular greyish band, tapering towards anal angle. The underside agrees with the upper side.

Antennae black, fairly long, strongly bipectinate to the apex. Palpi and body as ordinarily in *Nyctemera*; abdomen above grey, with the posterior borders of tergites whitish or yellowish.

The species comes very near *hyalina* B.-Bak, from Arfak Mts., 4000 ft., New Guinea, of which I saw the ♂ type-specimen in the British Museum.

The male genitalia (fig. 14) are remarkable on account of the extremely slender uncus + tegumen and the simple valvae, which are rather short but end in a long, somewhat clavate process, which is turned up. The lower margin of valva is duplicated; the inner margin has a broad process directed inwards like an auricula, but it is a little removed from the base of the valva. The aedeagus is rather short, straight and simple.

Two ♂, holo- and paratypes, 44 and 46 mm. expansion, both from the Minahassa, N. Celebes, in coll. Van den Bergh, Zool. Museum, Amsterdam. One ♂, paratype, 48 mm., Malino-Goa, Celebes, 1100 m., leg. Kalis, coll. Wageningen. This male has the white band in fore wing a little narrower, but no doubt represents the same species.

One ♀, allotype, 53 mm., G. Lampobattang, 1500 m., leg. Kalis, May, 1938, coll. Wageningen. This specimen agrees well with the described males, but has the antennae less strongly bipectinate, the branches of the joints tapering towards the apex and not reaching it.

2. **N. lugens** sp. n. (Pl. 2, fig. 5).

♂. Wings sooty black, fore wing with a narrow white transverse band, interrupted by some black veins and reaching from costa to n_2. In the paratype this band is a little narrower, consisting of some white spots, the spot in c_2 being the largest. In the hind wing the black colour is confined to a very broad marginal band, covering about the outer half of the wing, the rest of the hind wing being pure white, with some grey scales just at the base.

The male genitalia are exactly of the same type as in *N. crameri* Roepke from Java, as described in the preceding pages (cf. p. 53), showing clearly that both species belong to the same group. The similarity is so great that one might be inclined to consider *lugens* as a subspecies of *crameri* if their general aspects were not so divergent.

♀. Unknown.

Two ♂, holo- and paratype, both 39 mm., Todjambu, Central Celebes, 1936, leg. Toxopeus ; in coll. Wageningen.

3. **N. limbata** sp. n. (Pl. 2, fig. 2, text-fig. 9).

♂. Fore wing light greyish brown, semi hyaline, with a narrow, white, transverse band from costa to inner margin ; in c_2 it is slightly enlarged, including here a small patch of the ground-colour. At inner margin a small white patch near inner border of marginal band. Hind wing with a broad marginal band of the light greyish brown ground colour and an irregular median band, beginning broadly at costa, tapering towards anal area, not reaching anal margin. The latter to n_{1b} light greyish. Under side the same as upper side. Antennae black, moderately bipectinate, tapering towards tip. Head, patagia, tegulae and notum light yellowish, with black dots. Abdominal tergites greyish with the hind borders whitish yellow. Anal tuft light brownish yellow. Legs uniformly light greyish.

The genitalia of this specimen (fig. 9) are peculiar. The tegumen is triangular, the uncus long and slender, pointed, somewhat directed downwards. Aedeagus straight, with some dark chitinous teeth and some other dark structures in its interior. The valva is longer than broad ; it consists of an upper and a lower part, the former more strongly chitinized, blunt, with some small teeth along its free margin ; the latter thickly hairy over its entire length. Near base of upper margin a prominent hook-shaped appendage, auricula, densely covered with long, straight hairs. The internal structures in the aedeagus and the strong hairy appearance of valva characterize these structures sufficiently.

One ♂, holotype, 47 mm., Malino, 1100 m., Goa district, C. Celebes, June, 1936. Probably collected by Mr. Kalis, though I received it from another person. In coll. Wageningen.
♀ Unknown.

4. *N. infuscata infuscata* Hopffer (Pl. 2, fig. 4 ♂♀, text-fig. 11).

Hopffer, 1874 : 44 ♂ : N. Celebes. Snellen, 1879 : 73 ♂♀ : Celebes. Pagenstecher, 1897 : 439 ; id., 1901 : 129. Swinhoe, 1903 : 70 (*subvelata* Walker). Seitz, 1915 : 269, pl. 29*f* ♂ (*velans* nec Walker ?). Bryk, 1937 : 85 (*velans* nec Walker ?).

Mr. Nieuwenhuis, of Rotterdam, has received a large series of a very dark *Nyctemera* from Nulion, Banggai Archipelago, near Celebes, consisting of females only, with the exception of two males. This species seems to be the most common *Nyctemera* in that region. I think that it belongs to *infuscata* Hopffer, from N. Celebes, some similar specimens being in the Leiden Museum under the same name; furthermore, I have a series of this insect from Central Celebes, with the white discal markings in both wings more prominent. Swinhoe (1902), Seitz and Bryk ascribe it to *velans* Walker (1864 : 200 ♂ : Celebes); the former figures Walker's type-specimen, but from this figure I get the impression that *velans* and *infuscata* are not the same. *Velans* has the outer margin of fore wing less oblique, and the entire pattern of both wings is rather different. Seitz also figures what he calls *velans*, on pl. 29 f ♂; this figure fits better with our specimens from Banggai, but does not agree with Swinhoe's figure of Walker's type-specimen. In 1903 Swinhoe identified it with *subvelata* Walker, also from Celebes, considering *velans* as a different species. In order to clear up the situation a photograph of a pair from Nulion is reproduced here (Pl. 2, fig. 4); this needs no further explanation.

The genitalia of one of the two males were examined (fig. 11). They reveal the interesting fact that this species undoubtedly belongs to the *tripunctaria* group, the genitalia of both showing the greatest resemblance (cfr. text-fig. 8), though the moths have not the slightest similarity. Most authors even place them in quite different groups of the genus *Nyctemera*. The similarity of the two genital structures, however, is so striking that one should rather be inclined to consider *infuscata* as a subspecies of *tripunctaria*.

5. *Nyctemera clathrata clathrata* Vollenhoven (Pl. 2, fig. 8 ♂♀, text-fig. 10).

Vollenhoven, 1863 : 48 ♀ (*Leptosoma clathratum*): Amboina. Van Eecke, 1927 : 222 : Amboina, Morotai.

Snellen van Vollenhoven's type-specimen in the Leiden Museum is a fairly well-preserved female, on an old, large pin and not set up. There is a second specimen in this Museum, a male from Morotai, already mentioned by Van Eecke (*l.c.*). I have a male and a female from Tobelo, Halmaheira, leg. Van Dijen; the male measures 41, the female 43 mm.; both are figured here; they agree well with the authentic material in the Leiden Museum. I am sure that Van Eecke is right when he says that all authors misunderstood this species, probably because they were not acquainted with it, and that the figures as given by Pagenstecher and Seitz are wrong.

The insect is quite characteristic by the pattern on both wings, caused by the grey veins on the white background. In the hind wing a grey marginal band is present in the male; in the female the marginal area is broadly suffused with grey. The abdomen has the tergites light grey with a white fringe at hind margin; the underside is nearly white. Antennae in both sexes fairly strong bipectinate, black. The general coloration of the ♀ is a little darker than that of the ♂.

The male genitalia (fig. 10) show the uncus broadly dilated, strongly separated from the tegumen; its virtual top is very short, pointed. The aedeagus is rather long and stout, straight and simple. The valva is longer than broad; its apex is strongly bilobed; both lobes are of about equal shape. Near base of lower lobe a strong, short projection is implanted, at inner side of the valva.

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EXPLANATION OF PLATES.

PLATE 1.

(Approx. $\frac{4}{5}$ natural size.)

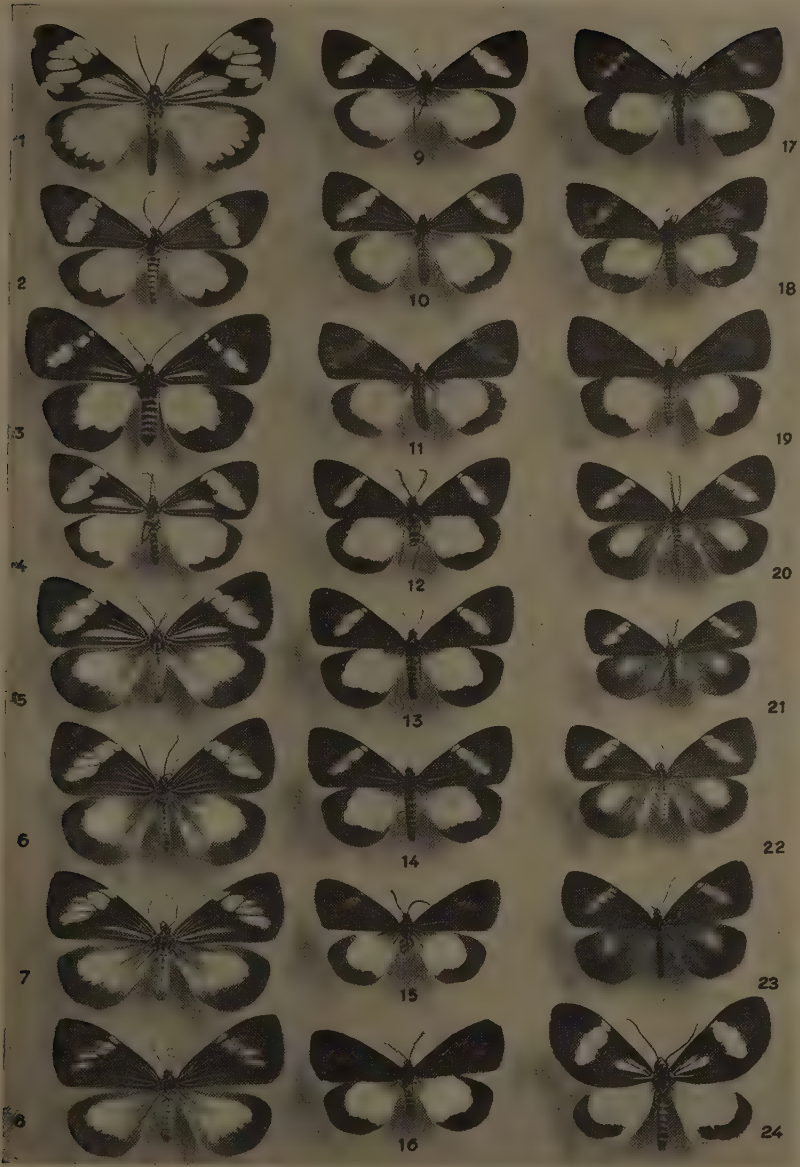
FIG.
1. *Nyctemera coleta coleta* Cr., ♂, Lawang, E. Java.
2. *N. baulus baulus* Boisd., ♂, W. Java.
3. *N. herklotsii herklotsii* Voll., ♀, Lembang, W. Java.
4. *N. latistriga latistriga* Walk., ♂, W. Java.
5. *N. tripunctaria tripunctaria* L., ♂, Depok, W. Java.
6. *N. t. tripunctaria* L., ♂, Java.
7. *N. t. tripunctaria* L., ♀, Tjisuru, W. Java.
8. *N. t. tripunctaria* L., ♀, Tjisuru, W. Java.
9. *N. crameri crameri* Rpke., ♂, Blawan, E. Java.
10. *N. c. crameri* Rpke., ♀, Idjen Plains, E. Java.
11. *N. popiya popiya* Swinh., ♀, Java.
12. *N. distincta* f. *anthracinum* Voll., ♂, Blawan, E. Java.
13. *N. d.* f. *anthracinum* Voll., ♀, Blawan, E. Java.
14. *N. d. distincta* Walk., ♀, Tjibodas, W. Java.
15. *N. popiya popiya* Swinh., ♂, Tjisuru, W. Java.
16. *N. p. popiya* Swinh., ♂, Pamegattan, W. Java.
17. *N. distincta distincta* Walk., ♀, G. Lawu, Centr. Java.
18. *N. d. distincta* Walk., ♀, Sukanegara, W. Java.
19. *N. popiya popiya* Swinh., ♀, G. Salak, W. Java.
20. *N. trita trita* Walk., ♂, Java.
21. *N. t. trita* Walk., ♂, Djampangs, W. Java.
22. *N. t. trita* Walk., ♀, Kubankankung, W. Java.
23. *N. t. trita* Walk., ♀, Pangendaran, W. Java.
24. *N. maculata maculata* Walk., ♂, G. Tjisuru, W. Java.

PLATE 2.

FIG.
1. *Nyctemera tenuifascia tenuifascia* Snell., ♂, G. Lawu, Centr. Java.
2. *N. limbata* Rpke., ♂, holotypus, Malino, Cel.
3. *N. latistriga* f. *nubecula* Voll., ♂, lecto-holotypus, Mus. Leiden.
4. *N. infuscata infuscata* Hopff., ♂♀, Nulion, Banggaai Isl.
5. *N. lugens* Rpke., ♂, holotypus, Todjambu, Centr. Cel.
6. *N. diaphana* Rpke., ♂, holotypus, Minahassa, N. Cel., Mus. Amsterdam.
7. *N. latistriga* f. *leucostigma* Vol., ♂, holotypus, W. Java, Mus. Leiden.
8. *N. clathrata clathrata* Voll. ♂♀, Tobelo, Halmahera.

(Figs. 3 and 7 are slightly enlarged, the others about natural size.)

The Society is indebted to Professor Roepke for his kindness in defraying the cost of these plates and for arranging to have them printed in Holland.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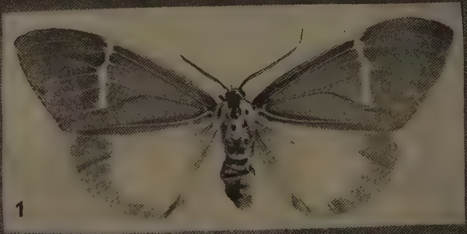

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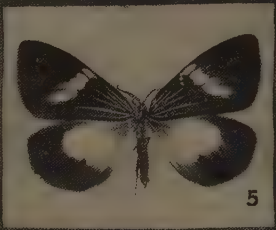

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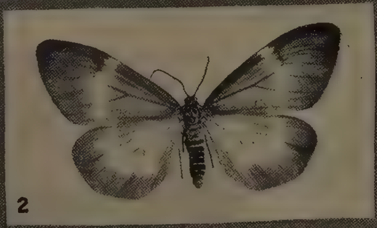

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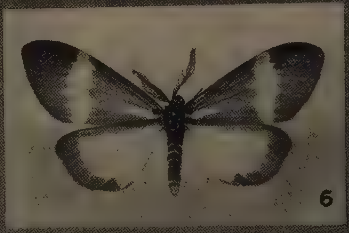

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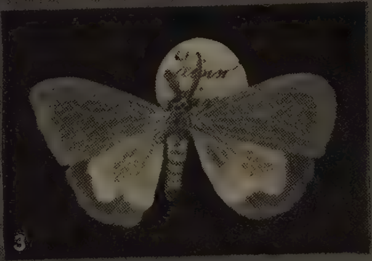

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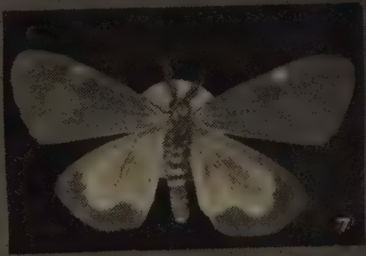

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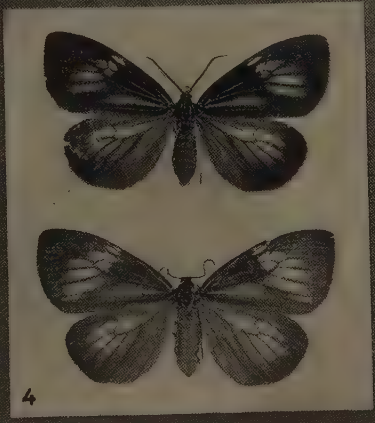

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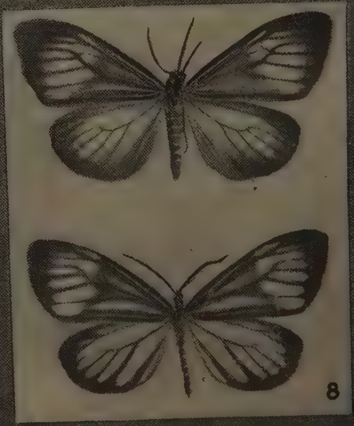

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W. Roepke The genus *Nyctemera* Hübner

Vol. 100. Part 3. Pp. 71–133, 8 plates, 28th July, 1949
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CONTENTS

	PAGE	
HALE CARPENTER, Emeritus Professor G. D., M.B.E., D.M. *Pseudacraea eurytus* (L.) (Lep. NYMPHALIDAE): A study of a polymorphic mimic in various degrees of speciation . .	71–133,	8 plates, 1 map, 2 tables, 28 figs.

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PSEUDACRAEA EURYTUS (L.) (LEP. NYMPHALIDAE): A STUDY OF A POLYMORPHIC MIMIC IN VARIOUS DEGREES OF SPECIATION.

By Emeritus Professor G. D. Hale Carpenter, M.B.E., D.M.
(*Hope Department of Entomology, University of Oxford.*)

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With 8 Plates, 1 Map, 2 Tables and 28 Text-figures.

> *Variation and mutation alone do not necessarily produce new species. After all, it is quite thinkable that such variation might lead only to a single, interbreeding, immensely variable community of individuals. But this is not what we find in nature.* Mayr, E., 1942. *Systematics and the Origin of Species.* Page 154. (Columbia University Press.)

The butterflies of which an account is given in this study seem to present an example of such a community.

		PAGE
I.	Introduction	71–72
II.	The genus *Pseudacraea*	72–74
III.	The species *eurytus* Linnaeus	74–76
IV.	Synonymy	76–84
V.	Male genital armature	84–88
VI.	Forms of *eurytus*, descriptive	88–105
VII.	Distribution of each form	105–116
VIII.	The mimetic relationships and their bearing on the theory of mimicry	116–127
IX.	Acknowledgments	127–128
X.	Bibliography	128–133

This study is based on personal experience of the species in Uganda, on my own examination of 1663 museum specimens, and on MS. or published records of 221 other specimens, total 1884.

I. Introduction.

Pseudacraea eurytus (L.) can justly dispute with *Papilio dardanus* Brown the distinction, conferred upon the latter by E. B. Poulton, of being "the most interesting butterfly in the world."

Both frequent light forest, or thick bush, in most parts of Africa, where such an environment is found, from the West Coast to Abyssinia, East and South-East Africa. The *Papilio* occurs in Madagascar, and a close ally in the Comoro Isles, but the Nymphaline is unknown from those localities. Both occur on the islands of the Gulf of Guinea, and the *Papilio* on Zanzibar and Pemba, but the *Pseudacraea* is not known from those two islands. Neither have yet been found in Southern Arabia, zoologically part of the Ethiopian region although *dardanus* occurs on the Golis mountains of Somaliland.

Both are wonderful mimics, and here the *Papilio* must certainly yield the palm to the Nymphaline, which is incomparably superior. The models are found in the Danainae for *dardanus* and the Acraeidae for *eurytus*, in the first case two genera being concerned (*Danaus* and *Amauris*), in the second the genus *Bematistes* only.

The form of *Papilio dardanus* in Madagascar is sexually dimorphic to a minimal degree and is believed to represent the ancestral form. On the continent *dardanus* occurs in several races, of which the females, tailless, differ from the males by being mimetic. A primitive, male-like, female exists in Abyssinia, with others showing rudimentary mimetic pattern and tails in varying degrees of reduction.

In the highlands of Kenya Colony the females are extremely variable; hardly two are alike, and the stages of development of the fully mimetic form from the male-like, non-mimetic form, can be clearly traced.

Pseudacraea eurytus, on the other hand, is an equally perfect mimic in both sexes, but nothing is known as to its origin. Its forms may be sexually dimorphic or monomorphic, according to the condition of the numerous species of *Bematistes* which they mimic, sex for sex. Some forms are confined to the male, others to the female. One form of female, mimicking the female of a dimorphic *Bematistes*, by a change of colour (but not of pattern) is brought to resemble both sexes of another, monomorphic, *Bematistes*. In one locality there is only one species of model, sexually dimorphic, and the *Pseudacraea* corresponding to it is exceptional in that there are two colorations for the female. One resembles the female *Bematistes*, the other, together with the male, has the appearance of the male *Bematistes*.

The forms of *eurytus* were, of course, originally described as distinct species; they are often extremely variable, which is a frequent occurrence among mimics, and this variability has been closely studied in Uganda.

II. The Genus *Pseudacraea*.

The full synonymy is given later (Section IV).

Westwood (1850) separated from the hotch-potch of *Diadema* two subsections as follows: Discoidal cell closed in all the wings, which are thickly marked with a number of small black spots at the base on the underside. Those species with wings triangular were allotted to *Panopea* Hübner, namely, *semire* Fabricius, *lucretia* Cramer, *hostilia* Drury. Three with wings elongate we reput into a new subdivision for which the name *Pseudacrœa* was devised; these were *hirce* Drury, *euryta* Linnaeus, *boisduvalii* Doubleday. Westwood wrote of these six species: "The African species P. Lucretia, Semire and Hostilia indeed, agree tolerably well in general form and character with the typical species, but the style of their markings, especially on the underside of the wings, which are thickly spotted with black, is very distinct. The admission of these species, however, requires the introduction of P. Euryta, Hirce, and Boisduvalii, which, although possessing much longer wings (resembling, in fact, Acraeae much more than Nymphalidae), have their undersides very similarly marked, their veins similarly arranged, and their palpi and antennae also alike." It is interesting that Westwood, an opponent of the Darwinian explanation of mimicry, commented upon the resemblance to Acraeae in the length of the wings, but not the extraordinary likeness in colour and pattern, except for the basal spots.

The systematic position of the genus *Pseudacraea* requires further study. Aurivillius (1925), in the African " Seitz," makes no use of the section which Stichel, in the Palaearctic volume, calls Limenitidi, embracing *Neptis* and *Limenitis*. Fruhstorfer, in the Indo-Oriental volume, uses Limenitidi and Neptididi as two equivalent groups. Aurivillius, however, puts *Pseudacraea* in his section Nymphalinae (embracing *Cymothoë*, etc.), with Neptidinae next.

The egg, larva and pupa of *Pseudacraea eurytus* all suggest affinity with *Limenitis*. The male genital structure, considered in detail in Section V, has a certain resemblance to that of some of the Oriental *Limenitis*, less to that of the American and European species, and African species of *Neptis*. Thus it is at present difficult to say from whence *Pseudacraea* is derived ; it seems rather isolated.

There is in Madagascar an endemic species, *glaucina* Guenée, non-mimetic, with green spots which in *Pseudacraea* are only matched by *semire* Cramer, ranging from West Africa into Uganda. These are the only non-mimetic species, for even *hostilia* Drury has a generalized Acraeine appearance on the underside. Now it is of interest that the aedeagus of *glaucina* departs in one respect from those of all other species of *Pseudacraea*, and in this respect approaches *Limenitis*, of which all the Oriental species examined have an aedeagus different from that of *Pseudacraea* (see Section V).

Mimicry in the Genus Pseudacraea.

The following table gives the mimetic relationships of the species, excluding the forms of *eurytus*, which are considered in detail later, and the two non-mimetic species *glaucina* and *semire*:

(A) Species mimicking Danainae.

Mimic.	*Model.*
Ps. poggei poggei Dewitz	*Danaus chrysippus aegyptius* Schreber.
,, ,, *carpenteri* Poulton	,, ,, *dorippus* Klug.
,, *lucretia* forms	*Amauris* spp.
,, *deludens deludens* Neave	,, *echeria lobengula* E. Sharpe.
,, ,, *echerioides* Talbot	,, *albimaculata interposita* Talbot.
,, *dolomena pharsa* Fruh., (♀ = *dolichiste* Hall)	,, *niavius dominicanus* Trimen

(B) Species mimicking Acraeidae.

Mimic.	*Model.*
Ps. eurytus forms	*Bematistes* spp.
,, *gottbergi neumanni* Thureau	*Bematistes poggei nelsoni* Grose Smith
,, ,, *gottbergi* Dewitz	,, *elongata* Butler
,, *boisduvali boisduvali* Doubleday	*Acraea egina egina* Cramer.
,, ,, *trimeni* Butler	,, *zetes acara* Hewitson.
,, *clarki clarki* Butler	,, *orina orineta* Eltringham.
,, ,, *egina* Aurivillius	,, *egina egina* Cramer
,, *acholica* Riley	,, *perenna* Doubleday and Hewitson, or *A. egina*
,, *dolomena dolabella* Hall ,, *hostilia* Drury	A general Acraeoid appearance

It is seen that species of the one genus mimic species of four genera, two of which are Danaine and two Acraeid. It is interesting that the two Danaine genera and the Acraeid *Bematistes* are mimicked by *Papilio dardanus*, but by the female sex only, so that in this case the " parallelism " is limited to that sex.

III. The Species *Pseudacraea eurytus* Linnaeus.

The proverbial beauty of the " White Admiral " (*Limenitis camilla* Linnaeus), especially in flight, is shared by other Limenitids. Thus, in the discussion of *Limenitis bredowii* Geyer (Carpenter and Hobby, 1944, p. 324), reference was made to observations that it is " a warrior with a good deal of character " and " a regal butterfly of dignified demeanour and exclusive habits." The common name " Viceroy " in America for *Limenitis archippus* Cramer speaks for itself. As regards *Pseudacraea eurytus*, Fruhstorfer (1903) in his (unfortunately inadequate) description of the form *karschi*, wrote that it is an extremely dainty species, one of the noblest of this noble genus and particularly characterized by the delicate colour and bloom of the wings, which the most consummate artist could not paint more exquisitely. The sheen on the wings of a fresh *tirikensis* or *obscura* never failed to arouse admiration when I collected, and Eltringham (1910, p. 75) wrote : " The female *Ps. rogersi* has a blue iridescence which is visible on the upper surface of the wings when viewed in certain lights. This structural colour is also observable in some speciemns of the female of *Pseudacraea hobleyi* " [= *tirikensis*]. Seen alive, *eurytus* is obviously an aristocrat by comparison with its models, which look mean beside it. The alert bearing and graceful flight (like that of *L. camilla*), the fine head with large palpi and graceful antennae, the strongly marked black spots on the underside, all compare very favourably with those features in the models.

Pseudacraea eurytus, in my experience, frequents places in the forest where it can feed on flowering trees in the sun, and does not seem to frequent heavy dark forest, although Mr. T. H. E. Jackson, in 1946, found it not so uncommon in the Ituri forest at Beni as seems to be indicated by its scarcity in collections (Jordan, 1912). On the Sese Isles of Lake Victoria I found it would come out, in the evening sun, to the edge of the curiously sharply defined patches of forest on Bugalla and Kome Isles, and feed on the flowering bushes of *Harungana madagascariensis* Lam. (see fig., p. 72, in Carpenter, 1920*b*) in company with many other butterflies, including its models and other species of *Pseudacraea*. When collecting from such an assemblage I soon learnt to take the *Pseudacraea* first, for they were very shy and if disturbed never returned, whereas their models could often be picked off by hand and were not lost if a stroke of the net to catch *Pseudacraea* disturbed them a little. In short, the behaviour of *eurytus* corresponds with what theory demands of a true mimic in the Batesian sense ; moreover, they lack the toughness and vitality of their models, and have no strong odour.

The Development of Knowledge of the Conspecificity of the Forms.

Hewitson (1868) figured on one plate, as forms of *eurytus*, the male and female of *eurytus*, the female *ruhama* and the female *striata*. Trimen (1869, footnote to page 515) wrote : " After examining Mr. Hewitson's fine series of this butterfly I am disposed to agree with him that it is at present impossible to separate the numerous forms which he has figured, with the exception of the female shown in the second plate, fig. 29, which appears to be a distinct species." It is, in fact, *Bematistes epiprotea* Butler.

Hewitson (1872) described *Diadema ruhama*, male, as allied to *D. eurytus* and *D. dolomena*. Butler (1873) described *simulator* as allied to Trimen's *imitator*, and in 1874*a* described *striata* as " quite distinct from *Pseudacraea euryta*." But he also describes " another form figured by Mr. Hewitson (pl. 3, fig. 8) so evidently a mimic of my *Planema elongata* that I cannot resist naming it *Pseudacraea metaplanema* n.sp." This was the female of *ruhama*. In the same paper Butler describes a female as "*Pseudacraea epigea*, n.sp. . . . possibly only a second form of the female " of *Pseudacraea* "*euryta*."

Aurivillius (1891), while he ascribes Butler's *metaplanema* to *ruhama*, yet thinks that *ruhama* and *theorini* differ from the others, considered as *eurytus* by Hewitson, by the transverse band of the fore wing running towards the posterior angle. It was by this longer oblique bar that in 1898 he divided the " species " into two main groups.

Haase (1892, p. 42) cites several forms, and states that their right to be regarded as separate species must be determined by breeding.

In 1894 Aurivillius placed *consanguinea* as a form of *theorini*. Not until 1911 was any further consideration given to the conspecificity of these forms, when Jordan, from study of genitalia and of transitional coloration and pattern concluded that there was no specific difference between western, eastern and southern forms. Poulton (1912*d*) wrote : " Dr. Jordan's discovery . . . led to the remarkable conclusion that the sexually dimorphic *Pseudacraea hobleyi*, mimicking the sexually dimorphic *Planema macarista* in the Entebbe district, was the same species as the two monomorphic Pseudacraeas flying in the same forests with it, viz. *P. terra* and *P. obscura*, mimicking respectively the sexually monomorphic *Planema tellus* and *P. paragea*." Poulton (1911, pp. 496–8) supported Jordan with evidence from the large collection made by C. A. Wiggins at Entebbe, in which there were specimens intermediate between *hobleyi* and *terra*, and between *terra* and *obscura*.

During 1911–1913 I was living on the Sese Islands of Lake Victoria, first on Damba, and then on Bugalla, and found Pseudacraeas abundant and variable, with many intermediates between the above-named forms. Moreover, different forms were seen flirting with each other, though never *in copula*. Thus, *hobleyi* ♂ pursuing *terra* ♀, *terra* ♂ pursuing *tirikensis* (= *hobleyi* ♀) and *obscura* ♂ the ♀ of *terra* (Poulton, 1912*a*–*d*). Having been urged by Poulton to obtain synepigonic series I kept a look-out for ovipositing females, and on June 16th, 1912, saw a female, intermediate between *obscura* and *tirikensis*, deposit an egg on a sapling (Poulton, 1913*a*, p. cxv) which, when reared, produced a *terra* (Carpenter, 1912). Subsequent families, bred from known parents, firmly established the conspecificity of the chief Uganda forms *terra*, *obscura*, *hobleyi* and *tirikensis* (Carpenter, 1912, Appendix by Poulton ; Poulton, 1913*b*, *c*), and study of large collections from Bugalla Island (Carpenter, 1914) revealed many transitional specimens. Unfortunately, no breeding has been done outside Uganda except in Durban, where there is only the one form, *imitator*. Schultze (1920) thought that *eurytus*, *striata* and *ruhama* would prove to be conspecific when bred ; he found *eurytus* ♀ in places frequented by *ruhama* ♂, and variations which suggested that *theorini* was of the same species.

The Immature Stages.

The first account of the life history was by Margaret Fountaine (1911) and concerns *imitator*. The larva when young feeds at the tips of the leaf, leaving the bare mid rib on which it rests. The figure shows paired spines, with the longest pair, branched at the tips, on the second thoracic segment projecting forwards on each side of the head. It fed on a Sapotaceous tree, *Chrysophyllum natalense* Sond. The pupa is long and thin, with long cephalic processes and a pronounced dorsal projection, flattened at the sides and curved at the summit. A full description of the life history of the first Uganda specimen to be reared was given by Carpenter (1912) and illustrations of the larva and pupa can be found in Carpenter (1920*b*, p. 262). The ovum was spherical but slightly flattened at the point of attachment, and at first is dull yellow; the surface deeply sculptured into hexagonal cells. The first stage larva was dull greenish white, the head smooth shining black, and there were no processes whatever on the body or head. Immediately after hatching, before eating any part of the leaf, though it had eaten the eggshell, it took up a position along the edge of the leaf, and within a few hours had affixed pellets of excrement to its back. When feeding it ate so as to leave a lateral vein of the leaf intact, still attached to its base, and rested on this bare rib, accumulating pellets of excrement on its back and around itself. The food-plant is a species of *Chrysophyllum* near *kayei* S. Moore. The first ecdysis produced a complete change in appearance and habits. The coloration became green and brown, with the posterior segments ashy grey. Paired spines arose on each segment, largest on the second. There was no change until the fourth ecdysis, the larva always resting at the tip of a bare rib and returning thither after feeding. When resting, the head and first five segments are raised from the leaf, and all that part behind the fourth pair of claspers is held up at a sharp angle, thus emphasizing the lateral ashy colour of that part of the body. The larva is very sluggish and rarely moves except for feeding. After the fourth ecdysis there was a great change in appearance; the general colour was velvety purplish brown, and the spinous processes were enlarged, those on the fourth to ninth segments being trifid at the extremity. Those on the second segment became very thick and diverged upwards, outwards, and then forwards. The last pair became very large and almost leaf-like owing to lateral flattening. The green pupa corresponded with that of *imitator*. The long cephalic processes, immediately after the last larval ecdysis, were short, curved dorsally, and quite separate from each other. They, with the dorsal abdominal processes, became straightened out into their final shape, apparently by distension with fluid.

IV. SYNONYMY.

The literature concerning the species under investigation has proved to be very involved owing, firstly, to differences in interpretation of and by the early authors. Secondly, many writers chiefly concerned themselves with coloration and hence often failed to distinguish between model and mimic. Thirdly, sexual dimorphism led to different conclusions according to whether the approach was made from consideration of the male or female; in the latter case a number of Acraeines were available which could be confused, but in the former only one. It is obvious that in some cases authors had not studied the works to which they refer, of which the plates show obvious differences. It has, therefore, been necessary to pay considerable attention to Acraeine synonymy until the date when the two categories had been clearly differentiated.

A. *Generic name.*

The original name for the species was *Papilio Barbarus Eurytus* Linnaeus (1758); this became (Linnaeus, 1764) *Papilio Heliconius Euryta.* Godart (1819) used the name *Acraea* (Fabricius, 1808) for insects wrongly included under *eurytus* by Cramer (1779), who mis-spelt it *Eurita.* Hübner [1819] founded the genus *Actinote* for four species among which was included Cramer's *Eurita*; he also founded *Panopea* for two other closely related species, but it was preoccupied for Mollusca (Ménard de la Groye, 1807). Doubleday (1845) placed *Euryta* under *Diadema* (Boisduval, 1832); this was preoccupied for Crustacea (Schumacher, 1817).

The new name *Planema* devised by Doubleday (1848) for a subgenus of *Acraea* included *Euryta,* and thus perpetuated the confusion caused by Cramer.

Westwood (1850) proposed *Pseudacraea* as a new subgenus of *Diadema* for three Nymphaline species, of which two were *Hirce* and *Euryta*, thus separating these from *Panopea,* also given subgeneric rank. Trimen (1869), however, combined these two groups under *Panopea.* Butler (1870) elevated *Pseudacraea* to a genus. Scudder (1875) selected *Euryta* as the type of Hübner's *Actinote,* but Hübner had adopted Cramer's interpretation of Linnaeus' name. That is to say, Hübner used *Actinote* for two species of Acraeine, thus continuing Cramer's mistaken usage of the name *eurytus.* The interpretation of Scudder's designation of *Euryta* as a genotype in either the Linnaean or Cramerian sense is governed by opinion 168 of the International Commission on Zoological Nomenclature, which provides for such cases being submitted to that Commission for a decision. Acceptance in the Linnaean sense of Scudder's designation would result in the transference to a Nymphaline of the generic name *Actinote* hitherto by common usage applied to Acraeines. Hemming (1936) prepared the case for the cancellation of Scudder's designation and a formal recommendation to this effect was submitted by Hemming and Riley (1946) to the International Commission on Zoological Nomenclature. Mr. Hemming has kindly informed me *in lit.* (dated 22.viii.48) as follows: "I can now tell you that the Commission considered this case (which was submitted to it by Riley and myself jointly) at its recent meeting in Paris, and agreed to use its plenary powers to cancel Scudder's designation of *Papilio eurita* Cramer (*recte Papilio eurytus* Linnaeus, 1758) as type, and to declare *Papilio thalia* Linnaeus, 1758) as the type of *Actinote* Hübner, [1819]." Scudder also (1875) designated *Hirce* Drury as the type of Westwood's genus *Pseudacraea*; it is now clear that *hirce* is the male of Linnaeus' *eurytus.*

B. *Trivial name.*

The first description (Linnaeus MS., 1751, in Aurivillius, 1882), the first published description (Linnaeus, 1758), and the first figure (Clerck, 1764) all referred to black and white females.

Linnaeus MS., 1751: "Papilio fuscus alis fascia alba, nigro-striatis, posticis punctis 10 atris.—Magnitudo media.—Alae rotundatae integerr. fuscae. Alae anteriores supra fuscae, fascia transversa alba brevis in medio; macula striata alba ad marginem interiorem; maculae 6 s. 7 versus basin; subtus similes. Alae posticae supra fuscae basi ferrugineae; disco versus basin albo, striis longitudinalibus nigris; puncta atra versus basin 9 s. 10.

"Corpus nigrum. Caput et thorax punctis albis adspersa. Abdomen subferrugineum punctis nigris."

Linnaeus, 1758: "Eurytus. 180. P[apilio] B[arbarus] alis integerrimis rotundatis concoloribus fuscis nigrostriatis: fascia alba; posticis punctis decem atris. 3."

"*Habitat in* Indiis.
Alae posticae *basi ferrugineae, disco versus basin albo striis nigris*."

The MS. description by Linnaeus clearly refers to the Nymphaline in the collection of Queen Ludovica Ulrica which was figured by Clerck and is still extant. The 1758 description omits the abbreviation "M.L.U.," which is used in the diagnoses of other species, such as No. 164 *Phidias*, to signify their presence in the Queen's collection. Thus we have no certain knowledge of the material that he was considering when framing the 1758 description apart from that provided by the internal evidence of the description itself which is on the same general lines as that of 1751. The published description omits the important phrase "maculae 6 s. 7 versus basin" from the account of the fore wing, thereby making it possible to contend that Linnaeus was not considering the Nymphaline. On the other hand, referring to the hind wings, he uses the words "punctus decem atris," which, as Aurivillius (1882) says, must be taken to refer to the Nymphaline.

Therefore Linnaeus (1758) seems to us to have adapted his 1751 MS. description to cover composite material. Collaborating with Clerck (1764) in his study of the Queen's collection he restricted the name *eurytus* to the Nymphaline which was illustrated, and also in his published account (1764) of the same material, which he elaborated by pointing out that there are two distinct white areas on the fore wing. It should be noted that Linnaeus first wrote *eurytus* and afterwards *euryta*. The following notes, kindly supplied by the Rev. Prof. L. W. Grensted, D.D., concern the spelling of the name. "The name should be written *eurytus* and not *euryta*. It is not an adjectival form, but a proper name, used of a king in Ovid (*Metamorphoses* **9**: 356) and of a centaur (*Metamorphoses* **12**: 220) and therefore stands in apposition to the generic name and does not take its gender. Parallel cases are *Maniola tithonus* L., *Coenonympha pamphilus* L." The description in the twelfth edition of the *Systema Naturae* (1767), because of the references, obviously applies to the Nymphaline black and white female. Müller's German version (1774) of Linnaeus (1767) calls the insect "Der Schwarzstrich." Fabricius (1775) quotes the 1767 description almost verbatim, and also refers to the 1764 account which has just been shown to apply to the Nymphaline. His reference to Seba's (1765) figure as representing *euryta* is therefore rather odd, seeing that it depicts a completely different butterfly from a Dutch colony in America. Appeals to competent authorities at the British Museum (Nat. Hist.), American Museum of Natural History, and the Amsterdam Museum, have failed to establish its identity. Fabricius' error is corrected by Goeze (1779), who gives *Euryta* the name " Zehnpunkte," and by Herbst (1790).

Cramer (1779) establishes the trivial name *epaea* for the brown male now considered to be the model. He figured a black and white female, now known as *Bemastistes umbra macaria* F., as equivalent to the *eurytus* of Linnaeus, but adds for the first time a supposed male, which is in fact a female *Bematistes* of a different subspecies, now known as *Bemastistes umbra umbra* Drury. Cramer's work, published in parts (Sherborn, 1902, *Index Anim.*, Sect. prim., xx) bears the date 1782 on the title-page. Some later authors appear not to have recognized this fact, which has an important bearing on the priority of names, notably *epaea* vis à vis *gea*. Fabricius (1781) in regard to *euryta* makes no advance on his previous publication. He describes a brown male as *gea*, but there is intrinsic evidence from the wording that the description is composite ; thus the subapical spot of the fore wing is stated to be " interdum divisa ad apicem," which suggests both Acraeine and Nymphaline. He writes also of the insect itself " variat interdum basi omni alarum nigro punctata," a phrase which has almost the appearance of an afterthought and has apparently led some authors, who did not regard the last sentence as part of the original description, to restrict the name to the Acraeine, which will be shown to be Cramer's *epaea*.

Drury (1782) establishes the name *hirce* for his figure of the male Nymphaline and alludes to the black spots at the base of the fore wing by which it is now known that the Nymphaline is readily distinguishable from the Acraeine. Jones (1784, unpublished ; with later annotations) figures a male Nymphaline as *hirce*, which he equates, rightly in part, with the composite *gea* of Fabricius. He also considers his own figure of *hirce* Drury to be the same as Cramer's figure of *epaea*. This is clearly wrong, because Cramer's figure does not show Drury's basal fore wing spots and does show division of the subapical spot. Jones also figures two other butterflies similar to those illustrated by Cramer (1779) as "*eurita*," but thinks that they represent different species, applying Drury's name *umbra* (1782) to the brown " male " [*recte* female] while retaining Cramer's application of the Linnean name *eurytus* to the black and white female [*macaria*].

Fabricius (1787) after his revised description of *euryta* cites Cramer's figures, but mistakenly includes a third figure C, which represents a Pierid. He had previously (1775) cited the accounts by Linnaeus (1764, 1767), which certainly embraced the Nymphaline but, influenced by Cramer, he now omits from his account of *euryta* everything that might result in the inclusion of a Nymphaline under that name.

Gmelin's thirteenth edition of Linnaeus (1790) repeats the last Linnean description with minor verbal differences, citing in addition references to Fabricius without correcting his errors. Herbst's interpretation (1790) of *eurytus* as indicated by his figures and descriptions is that of Cramer. His lack of critical discussion of his references, one of which is to Clerck's figure, shows that like Fabricius and Gmelin he failed to appreciate that the name *eurytus* had been applied to Nymphaline and Acraeine. Fabricius (1793), discussing *euryta*, quotes the first part of his 1775 description and publishes as a synonym the name *timandra*, which he had applied in MS. to Jones' figure (1784, **2** : pl. 25), then considering it to be a new species. This figure he now thinks represents *euryta*, whereas it actually depicts a female *epàea* Cramer, the model. He further confuses the issue by citing Cramer's figures [*recte u. umbra*, *u. macaria* and a Pierid, *Delias thysbe thysbe* Cramer] and those of Seba.

In his consideration of *gea* the only references cited are two figures of Nymphalines, while in the description, by alluding to the subapical spot as being sometimes divided, he includes the Acraeine *epaea*.

Palisot de Beauvois (1805) accepts Cramer's interpretation of *euryta* and figures a female [*recte alcinoë*] which he equates with Cramer's female *euryta* [*recte macaria*].

Turton (1806) apparently follows Fabricius (1793), but cites only Cramer and Jones (1784, **2** : pl. 25). He repeats Fabricius' *lapsus calami* of including Cramer's figure of a Pierid. Godart (1819) accepts Cramer's conception of *euryta*, but points out that the habitat is " Sierra Leone " and not " les Indes." In regard to the males of the model (*epaea*) and mimic (*eurytus*) he perpetuates the previous confusion and introduces a new source of error by his citation of Fabricius' description of [*Acraea*] *jodutta* as the female of *epaea*, which he calls *gea*. Lucas (1835) adopts Godart's interpretation of *euryta*, namely, that of Cramer, but figures a female *alcinoë*, thus misidentifying Cramer's figure, which shows a female *Bematistes umbra macaria*. Westwood (1837) in his revision of Drury's previously mentioned work replaces *hirce* by the Fabrician name *gea* and couples it with a new description, applying solely to the Nymphaline figured. In the table of synonyms, which he does not discuss, he includes references to the males of both model and mimic and to *Acraea jodutta* as representing the female. Doubleday (1845) correctly distinguishes Clerck's *eurytus* as the true one, calling it *Diadema euryta*, differentiating it from Godart's *euryta*, which is the same as Cranmer's. He suggests that *hirce* is the male of Clerck's *eurytus* and describes it.

Doubleday (1848) having established *Planema* as the name of a subgenus, disentangles *epaea* from its Nymphaline implications and associates the brown male and white female as one species, which he calls *gea*. He points out that a specimen marked by Fabricius as *gea* in the Banksian collection has associated with it another butterfly, which is really *hirce* Drury and the male of *eurytus* Linnaeus. Under *Planema euryta* he puts Cramer's figure [*recte macaria* female] associating it with the male *macaria* of Fabricius. He correctly separates Cramer's supposed *eurytus* male as *Planema umbra*. He remarks that the confusion in the minds of previous authors, as far back as Cramer, could have been avoided by attention to anatomical details.

Westwood (1850) establishes *Pseudacraea* as a subgenus of *Diadema*, including *hirce* and *euryta* as separate species. Hewitson (1867) figures as *eurita* a number of species of Acraeine as representing variants of Linnaeus' *eurytus*, which he interprets in the same sense as Cramer. Further (1868) he uses the name *Diadema eurytus* for figures of a male and three forms of a female Nymphaline, rightly associating Drury's male *hirce* with Clerck's female *eurytus*. Hewitson's obscure allusions to " the typical variety described by Linnaeus " . . . " the typical specimen in the Linnaean cabinet " . . . " the Linnaean type " make confusion worse confounded. It may be said here that the female of *Bematistes umbra macaria* now in the collection of the Linnean Society at Burlington House bears a label in J. E. Smith's handwriting " Euryta 757. S. Leone F.B.," which indicates that it was collected by Smith's servant Francisco

Borone, who is known to have visited Sierra Leone, and added by Smith to Linnaeus' collection. It is not, therefore, a Linnean type.

Trimen (1869) considers *Acraea euryta* in the sense of Cramer and Hewitson and therefore suggests retaining " the appellation of *Hirce* for the *Panopea*." Butler (1870) uses *Planema* as a generic name for *gea* which he restricts to the Acraeine, specifying that the " supposed variety " of Fabricius is *Pseudacraea euryta*. He independently confirms Doubleday's (1848) association of the male *macaria* of Fabricius with the black and white female of Cramer, calling it *Planema euryta*. Kirby (1871) treats *Acraea euryta* as an Acraeine, citing many of the references already given for this interpretation and adds as variants *alcinoë* and *vestalis* (Felder, 1865). The male and female Nymphaline are named *Pseudacraea hirce*. Mabille (1876) refers to *Acraea euryta*, citing Palisot de Beauvois' figure [*recte alcinoë*] and adds that there are varieties other than those represented by Hewitson. The Nymphaline is discussed as *Pseudacraea hirce*. Plötz (1880) uses *Acraea eurita* in Cramer's sense and equates *Panopaea euritea* [sic] of Clerck with *hirce* Druce. Aurivillius (1882) gives an extremely important clarification of the confusion, establishing the Linnaean *eurytus* as a Nymphaline and segregating those authors favouring the Acraeine interpretation.

Mabille (1886) gives a figure of a female *alcinoë*, repeating Palisot de Beauvois' error of equating it with Cramer's female *macaria*. The occurrence of any species of *Bematistes* in Madagascar has never been confirmed. Tylor and Skertchly (1886) figure as "*Panopoea hirta* " a female of *Pseudacraea eurytus*, citing as its model a female *Bematistes alcinoë*, which they call *Acraea gea*.

Trimen (1887) still uses the trivial name *hirce* for both sexes of *Pseudacraea eurytus*. Möschler (1887) follows Kirby's comprehensive citation under *Acraea Euryta* L. Staudinger, Schatz and Langhans (1888) continue to apply the name *euryta* to an *Acraea*. Aurivillius (1891) maintains *eurytus* L. and *hirce* Drury as distinct species. Haase (1891) figures females of a Nymphaline and its model, calling them respectively *hirce* and *gea*. In 1892 he places *B. alcinoë* and *B. vestalis* and *B. umbra* under *Acraea euryta*, as varieties. The English edition (1896) mis-spells *euryta* as " *eurypta*." Schaus and Clements (1893) record a species as *Planema euryta*, citing Linnaeus' description (1764), oblivious of the fact that this description certainly embraced the Nymphaline. Karsch (1893) still continues the use of *Acraea euryta* L. by recording under that name a specimen like one of Hewitson's figures, which is really *Bematistes u. umbra*. Aurivillius (1893 : 49) in a footnote protests against the continued usage of "*Acraea Eurytus* L.," maintaining that in 1758 Linnaeus specified that the hind wings have ten black spots, a number smaller than that of any *Acraea* but characteristic of *Pseudacraea*. Oberthür (1893) discusses *Pseudacraea eurytus* and *hirce* as though they were different species, using the name *eurytus* for male and female specimens. He figures the female, equating it with Hewitson's figure 8 [*recte ruhama*].

Aurivillius (1898) gives a most useful synonymic list, with bibliography, including the species which have been discussed, thus clearing up the confusion and establishing the nomenclature for the future. He lists Butler's *epigea* and his own new *bicolor* as aberrations of *eurytus* L., but considers *imitator* Trimen, *simulator* Butler, *fulvaria* Butler, *ruhama* Hewitson, *theorini* Aurivillius, with its ab. *consanguinea* Aurivillius, and *striata* Butler as distinct

Table I.—*Synonymic History.*

Name used.	Author.	Date.	*Pseudacraea eurytus* (L.)		*Bematistes umbra macaria* F.		*Bematistes umbra umbra* Drury.		*Bematistes alcinoë* Felder.		*Bematistes vestalis* Felder.		*Bematistes epaea epaea* Cramer.		*Acraea jodutta* Fabricius.		Seba's figure.
			M.	F.	M.	F.	M.	F.	M.	F.	M.	F.	M.	F.	M.	F.	
Papilio Barbarus Eurytus	Linnaeus	1758		D		?								?			
,, ,, ,,	Clerck	1764		cF													
,, *Heliconius Euryta*	Linnaeus	1764		cDf													
,, ,, ,,	,,	1767		cDf													
,, ,, ,,	Fabricius	1775		cD													f
,, ,, ,,	Goeze	1779		cd													
,, ,, *Eurita*	Cramer	1779		cf		DF		DF									
,, ,, *Euryta*	Fabricius	1781		cd													f
,, ,, *Gea*	,,	1781	D										D				
,, ,, *Hirce*	Drury	1782	DF														
[*Papilio*] ,,	Jones [MS.]	1784	cFf										cf				
[,,] *Euryta*	,, ,,	1784		c		Ff											
,, ,, ,,	Fabricius	1787				Df		f									
,, ,, *Gea*	,,	1787	D										D				
,, ,, *Euryta*	Gmelin	1790		cdf		f		f									f
,, ,, ,,	Herbst	1790		cf		DFf		DFf									
,, ,, ,,	Fabricius	1793		cD		f		f						f			f
,, ,, *Gea*	,,	1793	Dff										D				
,, *Euryta*	Palisot de Beauvois	1805				f		f		DF							
,, ,, ,,	Turton	1806		D		f		f						f			
Acraea Euryta	Godart	1819		cf		Dff		Dff						f			f
,, *Gea*	,,	1819	cff										cDff		f	cD	
,, *Euryta*	Lucas	[1835]		cf		cD		cD		F				f			
,, *Gea*	Westwood	1837	cDFf										cf			c	
Diadema Euryta	Doubleday	1845		Df													
,, *Hirce*	,,	1845	Df														
Acraea (*Planema*) *Gea*	,,	1848											cf	f			
,, (,,) *Euryta*	,,	1848			c	cf											

Diadema Euryta	Doubleday	1848	cf	cf									
„ (*Pseudacraea*) *Hirce*	Westwood	1850	cf										
„ („) *Euryta*	„	1850		cf									
Acraea Eurita	Hewitson	1867		c	F	f	F	Fff	Ff	ff	ff	Ff	[NOTE.—Other species of *Bematistes* are also figured.]
Diadema Eurytus	„	1868	Ff	FFFf									
Acraea Euryta	Trimen	1869		c	f	f	f	ff	f		f		
Panopaea Hirce	„	1869	f	cf									
Pseudacraea Euryta	Butler	1870	cf	cf									
Planema Euryta	„	1870			cf	f							
Acreaa Euryta	Kirby	1871		c	cf	cf	f	cfff	ff	f	ff		
Pseudacraea Hirce	„	1871	cfff	cff									
Acraea Euryta	Mabille	1876								f			
Pseudacraea Hirce	„	1876	fff	ff									
Acraea Eurita	Plötz	1880				f		f					
Panopaea Euritea	„	1880	f	f									
Pseudacraea Eurytus	Aurivillius	1882		cff									
Acraea Euryta	Mabille	1886		c	c	cf		f		Ff			
Panopoea hirta	Tylor and Skertchly	1886		F									
Pseudacraea Hirce	Trimen	1887	f	f									
Acraea Euryta	Möschler	1887		c	cf	f	f	fff	ff		ff		
Pseudacraea Eurytus	Aurivillius	1891		cff									
„ *Hirce*	„	1891	ff										
„ „	Haase	1891		F									
Acraea Euryta	„	1892						c		c		c	
Planema euryta	Schaus and Clements	1893		c									
Acraea euryta	Karsch	1893						f					
Pseudacraea Eurytus	Oberthür	1893	f	Ff	[*recte* form *ruhama* Hew.]								
„ *Hirce*	„	1893	c										
„ *eurytus*	Aurivillius	1898	cfff	cfff									

species. It may be added that at a later date (1912, in Seitz) he admits the possibility that all these are conspecific.

Table I shows the synonyms of *Pseudacraea eurytus* L. and species confused with it. The names used by the authorities cited in the second and third columns are given in the first column. Our interpretation of the species embraced in these accounts is indicated by letters in the appropriate columns under their modern names. These letters have the following significance :

c, one or more citations to earlier accounts without figures.
d, repetition of an earlier description.
f, reference to a figure.
D, original or revised descriptions.
F, original figure.

V. THE MALE GENITAL ARMATURE.

Dr. Jordan (1911) came to the conclusion that the forms of *eurytus* which he examined showed no appreciable differences in the male genital structure.

A greater number of forms, over a wider area of distribution, has been examined during this study, and confirms Jordan's conclusion that there is no specific differentiation.

The general appearance of the armature is shown by fig. 5 ; the only parts that call for comment are the claspers (valves) and aedeagus. The former, in all forms of *eurytus*, are without any teeth ; they are simple elongated lamellae pointed at the distal end.

The aedeagus has a characteristic annular thickening around its distal end which, mid-ventrally, is elongated into a small upcurved papilla, well shown in lateral view in figs. 1 and 3, and from the dorsal aspect in fig. 4.

The same character is shown in other species of *Pseudacraea* (see figs. 10–18), although the annular thickening is not always clearly shown. A ventral view is given in fig. 14.

These other species of *Pseudacraea* show considerable differences among themselves ; the valves are quite simple in *semire* Cramer (fig. 10), but in *hostilia* Drury (fig. 11) and *dolomena* Hewitson (fig. 12) there are small teeth, which in *gottbergi neumanni* Thurau (fig. 14), *poggei* Dewitz (fig. 16) and *boisduvali* Doubleday (fig. 17) reach formidable proportions, while in *clarki* Butler (fig. 13) and *lucretia* Cramer (fig. 15) they are fairly large.

The valve, or clasper, in *boisduvali* has a unique structure in the form of a hook projecting downwards from a ridge on the inner surface and facing anteriorly. This, together with the shorter and deeper proportions of the clasper, quite separate *Pseudacraea boisduvali* from the other members of the genus. Lastly, *glaucina* Guen., confined to Madagascar (fig. 18) has valves not very dissimilar from those of *semire* (fig. 10), but the aedeagus seems to lack the annular thickening and has the papilla considerably developed so that it approaches the elongated shape of the end of the aedeagus in Oriental

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FIGS. 1–9, forms of *Ps. eurytus :* 1, *eurytus ;* 2, *fulvaria ;* 3, *terra ;* 4, *hobleyi ;* 5, *mimoras ;* 6, *victoris ;* 7, *rogersi ;* 8, *conradti ;* 9, *imitator.* FIGS. 10–18, other *Pseudacraea :* 10, *semire ;* 11, *hostilia ;* 12, *dolomena ;* 13, *clarki ;* 14, *gottbergi neumanni ;* 15, *lucretia ;* 16, *poggei ;* 17, *boisduvali ;* 18, *glaucina.* FIGS. 19–27, species of *Limenitis :* 19, *austenia,* Moore ; 20, *libnites,* Hew. ; 21, *lyncides* Hew. ; 22, *danava* Moore ; 23, *zayla* Dbldy. ; 24, *daraxa* Moore ; 25, *trivena* Moore ; 26, *lycone* Hew. ; 27, *lymire* Hew. All on same scale.

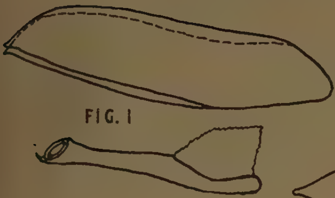


FIG. 1

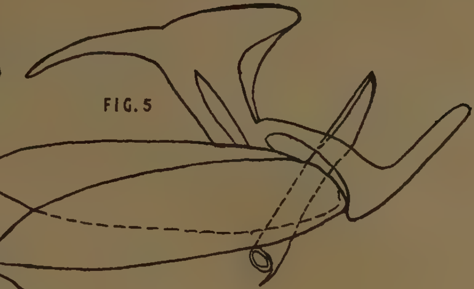


FIG. 5

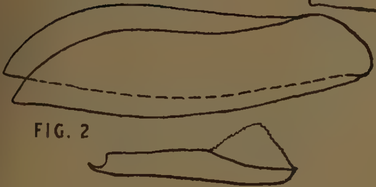


FIG. 2

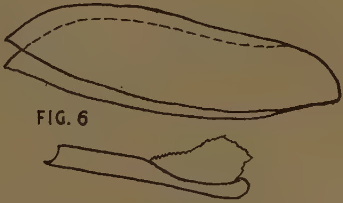


FIG. 6

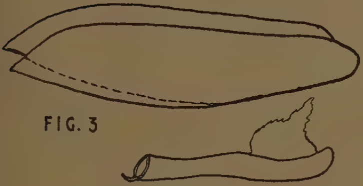


FIG. 3

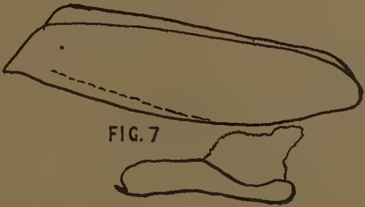


FIG. 7

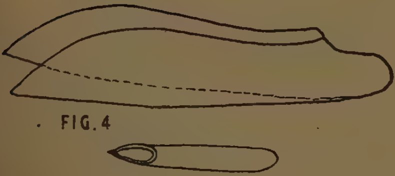


FIG. 4

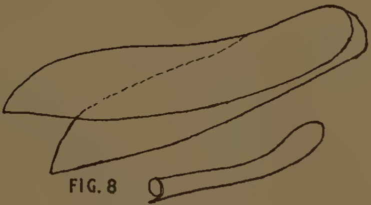


FIG. 8

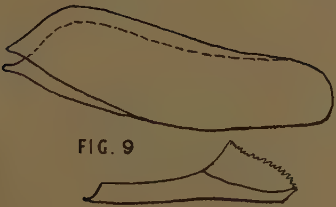


FIG. 9

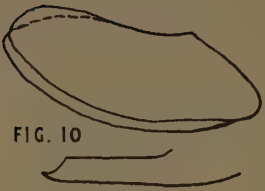


FIG. 10

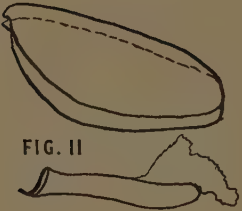


FIG. 11

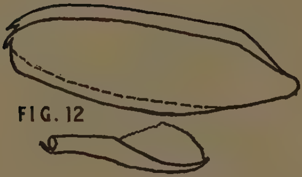


FIG. 12

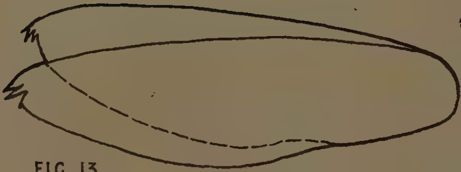


FIG. 13

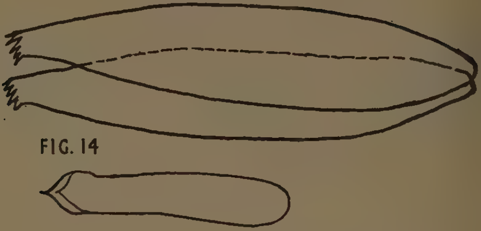


FIG. 14

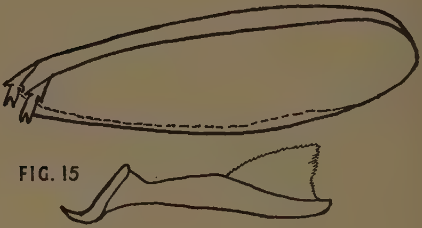


FIG. 15

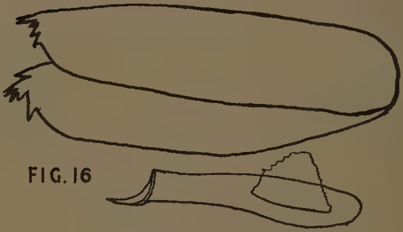


FIG. 16

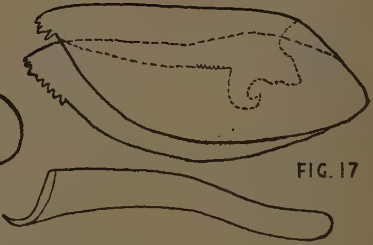


FIG. 17

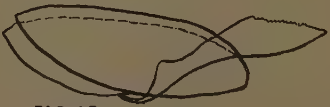


FIG. 18

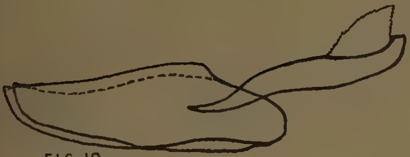


FIG. 19

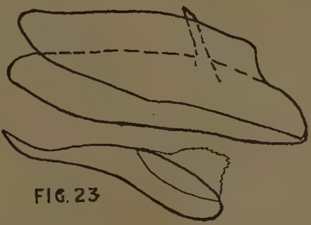


FIG. 23

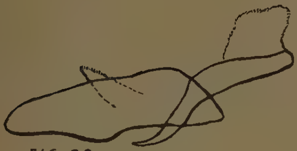


FIG. 20

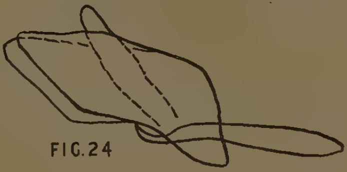


FIG. 24

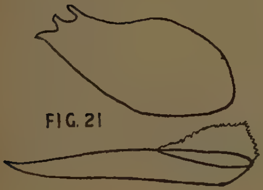


FIG. 21

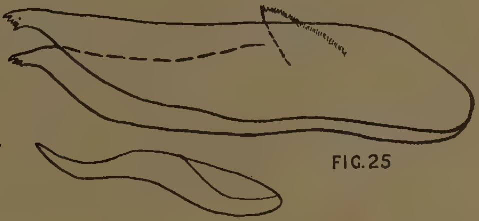


FIG. 25

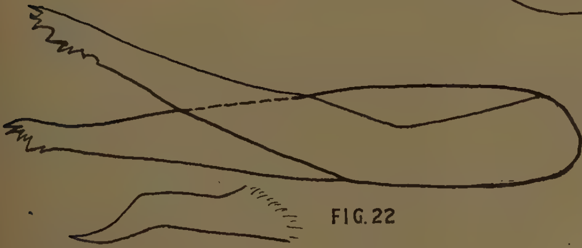


FIG. 22

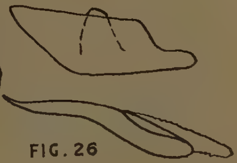


FIG. 26

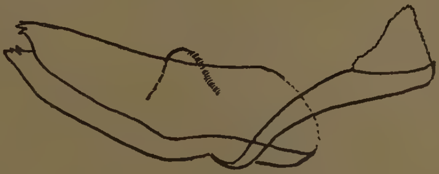


FIG. 27

species of *Limenitis* (cp. fig. 27). This may be a significant indication of affinity.

A number of Oriental *Limenitis* were examined to see if their genitalia throw light on the relationship of *Pseudacraea*.

The anatomy of some North American species was figured by Eltringham in Poulton (1914), and that of *L. bredowii* Geyer and of some species of *Adelpha* by Carpenter (in Carpenter and Hobby, 1944, p. 325). There is evidently little resemblance in the claspers, of which the humped outline is very different from that of *Pseudacraea*. The aedeagus was not figured. But in the species of Oriental *Limenitis* now figured the aedeagus shows generic difference from that of *Pseudacraea*; it lacks the annular thickening and papilla, and merely tapers gradually to a narrow elongated point, sometimes upcurved, sometimes straight. Some of these *Limenitis*, however, show some likeness to *Pseudacraea eurytus* in the simple, elongate, clasper, as in *L. austenia* Moore (fig. 19) and *L. libnites* Hewitson (fig. 20), while *L. danava* Moore (fig. 22) shows some likeness to *Ps. gottbergi neumanni* in the narrow form and distal teeth.

The structure on the internal surface of the clasper, to which attention was directed in Carpenter and Hobby (1944, pp. 324–5) is entirely absent from *Pseudacraea*, but present in various degrees of development in some Oriental *Limenitis* (figs. 20, 23–27).

Two European *Limenitis*, *camilla* L. and *populi* L. showed little resemblance to any species of *Pseudacraea* in their claspers.

It was thought that forms of *Pseudacraea eurytus* might be separable by female genitalia. A preliminary examination, however, showed that there was little difference between even two such distinct species as *eurytus* and *lucretia* and the subject was followed no further.

VI. Forms of *eurytus*.

The various forms of *Pseudacraea eurytus* will now be discussed seriatim: I have added a number of new forms to those which Aurivillius included in his "*Eurytus* group" (1898 and 1925). This was divided into two sections: (1) The front wing has two pale areas separated by a dark bar; one an oblique subapical bar, the other an inner-marginal patch of very varied size; occasionally the subapical band is absent. (2) The front wing has a median band, usually touching the apex of the cell, extending posteriorly beyond vein 3 and often reaching the inner margin and joining the pale area along that margin. If the band does not touch the cell it is more directly antero-posterior, and extends at least to vein 2. But it can be seen from the series of plates that this distinction is broken down by such intermediate stages as are shown on Plates I, III, IV, V, VII. Indeed, *Pseudacraea eurytus* provides many examples of what seems to be a deeply seated principle in pattern, namely, that a subapical dividing bar very readily breaks down or is thinned away so that the two separated pale areas become continuous. This can be seen even in the one form *rogersi* on Plate VII, figs. 61–63. The dividing bar seems to be a recent development not always stable. Other species, such as *Acraea jodutta* F. show the same variability, and *A. alciope* Hew. male, and *A. disjuncta* Smith show the rudiments only of the anterior part of this bar.

It is, in this connection, worth while referring to an observation on the development of the black pigmentation in the imago of *Papilio dardanus* Brown, a female of the form *hippocoon* F., which was noted while the colours developed a few hours before emergence. Colours begin to show through the pupal skin 24 hours before emergence of the imago; at first there is only a black rim around the front wing rudiment, but by degrees the black invades the central area and cuts off an apical from a basal white area (see Carpenter, 1914, *Proc. ent. Soc. Lond.* **1913** : liv). This would seem to be a case of ontogeny recalling phylogeny.

The general distribution of *eurytus* is shown by the map (p. 106), and it is of some interest that the first described, and therefore the nominotypical form, probably has the widest distribution. It extends from the River Gambia to northern Angola, well into the Congo, and along the mountains separating Uganda from the Sudan. The detailed distribution of each form will be given in a later section.

The ground colour of all the forms is fuscous, corresponding in most cases to the " Vandyke brown " of Ridgway (1912), but in some, especially the darker forms of female, is " bone brown." For future colour names the reference to Ridgway will be omitted, his name being simply given in inverted commas.

The pattern consists of a subapical oblique bar on the front wing beyond the cell and an inner marginal area; these may fuse, through the breaking down of the intervening dark bar, into a single band across the wing from costa to inner margin; in the form *striata* the band has disappeared. The hind wing shows a dark unspotted border of varying width with a central paler area. There is often a triangular basal area on the under surface of a strong reddish brown colour, which may also be shown on the upper surface. Five prominent rounded black spots in the cell of the front wing and another at the base of area 1*b* readily distinguish any form of *eurytus* from its model.

A number of smaller black spots at the base of the hind wing, while not exactly copying those of the models, give much the same effect. The long interneural dark streaks on the hind wing, finely pointed proximally, are a prominent feature; the presence of two of these in area 1*c* at once distinguishes a *eurytus* from its model or from other species of *Pseudacraea* except *dolomena* Hewitson, and this can be separated by the white rings around the spots on the front wing. The head and eyes are large as compared with the models, and the large palpi, yellow below with black tips, and black above, also aid identification. The long, graceful, antennae are very gradually thickened.

In the following account of the separate forms, which can be distinguished in this protean species, the form name alone will be used, to avoid wearisome repetition of "*eurytus*."

(1) *eurytus* L., 1758.

The name has suffered many changes in the older writings, having been written as *euryta*, *eurita*, *euritea* and even *eurypta*.

The female, which was the sex described by Linnaeus (see Plate VIII, fig. A) is figured on Plate VI, fig. 1, and the male, described as *hirce* by Drury, on Plate I, fig. 1 (see also figs. B1, B2). This form has also been figured by Clerck (1764, ♀, see figs. C1, C2), Drury (1782, ♂), Jones MS. (1784, ♂), Westwood (1837, ♂), Hewitson (1868, ♂, ♀), Tylor and Skertchly (1886, ♀), Haase (1891, ♀), Eltringham (1910, ♂, ♀), Aurivillius (1912, ♀). A remarkable aberration was figured by Jones

(1785) and is reproduced as figs. D1, D2, together with a photograph of Clerck's figure, for which I am indebted to Bodley's Librarian, Oxford, the book being in his charge (figs. C1, C2.) See Pl. VIII.

The pattern is the same in both sexes, except that the pale area of the hind wing in the female is contracted into a band across the basal half. The pale areas are " ochraceous tawny " in the male, pure white in the female. On the under surface of the female the base of the hind wing is occupied by a triangular area, coloured " orange rufous," extending half way along the cell and not quite half way along the costal margin. This highly important feature in the mimetic appearance, a characteristic aposeme in the model, will be known in future as the *basal triangle* ; it varies in extent and colour in the different forms. It is often much less developed in the male *eurytus*, and the figures of Drury and Westwood exaggerate it. On the upper surface in the female it is very poorly developed.

This form is, I think, the ancestral one from which others have been derived : its wide distribution through West Africa, and its present comparative invariability point to great age. There is, however, slight variability in the width of the dusky bar separating the pale areas on the front wing and in the male specimen figured on Plate I, fig. 2, this has broken down so that the two areas are continuous, producing an obvious stage in the transition to *ruhama* (fig. 5), through figs. 3 and 4. A male from Bitje was noted as having the subapical pale area very small. It is noteworthy that whereas in the male model the subapical area often has a small posterior portion cut off by a black partition, this is never the case in *eurytus*. The difference may have been the cause of the phrase "*interdum divisa*" used by Linnaeus, suggesting that in framing his description he had before him both model and mimic.

An interesting female in the Booth Museum, Brighton, from thirty miles south of Irumu in the Congo has the white areas slightly tinted yellow, especially on the inner margin of the fore wing and at the base of the hind wing. On the underside there is a well defined reddish brown basal triangle reaching to the middle of the cell but extending along the costa. This seems transitional to the form *jacksoni* described in this paper from Western Uganda.

The model for *eurytus* is *Bematistes epaea epaea* Cramer, sex for sex.

(2) *ruhama* Hewitson, 1872.

This variable form connects *eurytus* with *striata* : it was described from a male as " nearly resembling fig. 28 of *A. Euryta* in my *Exotic Butterflies*." This figure shows the species now known as *Bematistes elongata* Butler (see the table of Synonymy). A male *ruhama* corresponding to the type is shown on Plate I, fig. 5, and variants at figs. 3, 4, 6, 7, the last passing easily into *theorini* : the typical female is shown on Plate III, fig. 28, and variants at figs. 27 and 29 ; there is transition to *consanguinea* in fig. 27 and to *epigea* in fig. 29. The male has been figured by Aurivillius (1912) ; the female by Hewitson (1868) and Eltringham (1910), all in colour.

The chief character of the male *ruhama* is the narrow and only slightly bent transverse band on the fore wing from costa to vein 2, where it meets a vaguely defined "ochraceous orange" inner-marginal area, somewhat suffused with dusky scales. The greater part of the hind wing is of the same colour as the inner marginal area, and the dusky border is fairly well defined and narrow. There is no basal triangle, below or above.

In the female the pale band on the front wing is wider and the inner-marginal area is well defined and narrowed to become a continuation of the band behind vein 2. The anterior portion is " ochraceous buff," considerably paler than the posterior which, like the hind wing, is " ochraceous orange." There is no basal triangle. Butler's name *metaplanema* was applied to Hewitson's figure, one of his four forms of "*Diadema eurytus*," now known to be the female of the form *ruhama*. Schultze (1920) described as *ab. latefasciata* a female from South Camerun. The band is 12 mm. broad and extends basally into the inner part of the cell, and its margin is almost circular.

The male *ruhama* passes easily into *theorini* and so to *striata* by diminution of the transverse band: on the other hand such a specimen as is shown on Plate II, fig. 11, suggests that enlargment of the band, with condensation of the inner-marginal area to continue the band posteriorly, may be a stage in the production of *fulvaria*, as shown at fig. 12. The specimen illustrated at fig. 11 has the well developed basal triangle of *fulvaria* beneath, and a slight suggestion of a white discal bar, as in *fulvaria*.

The model for the form *ruhama* is *Bematistes elongata* Butler.

(3) *consanguinea* Aurivillius, 1894.

This is described as differing from the female of *theorini* by "having the entire basal half of the fore wing to the apex of the cell and the middle of vein 3 yellow brown; there is no distinct hind marginal spot; corresponds exactly to *Planema consanguinea* Auriv."

The figure of *Planema consanguinea* given by Aurivillius (1912) agrees well with the specimen figured on Plate III, fig. 26, which is obviously closely allied to *ruhama*.

(4) *striata* Butler, 1874.

This form has the least pattern of all the forms: it was described as having the front wings smoky brown with the interno-median area diffusely tawny; the hind wings tawny with a smoky brown outer margin.

A male agreeing with the type is shown on Plate I, fig. 10, and a female on Plate III, fig. 21. This form has also been figured by Hewitson (1868) Eltringham (1910) and Aurivillius (1925), all in colour.

The pale colour seems very slightly darker than the "ochraceous orange" of *eurytus* and *ruhama*, owing to thin suffusion with brown scales. On the under surface the basal areas are "ochraceous orange" while the periphery is much paler than the "Vandyke brown" upper surface, especially on the hind wing which may be decidedly whitish. This concentration of the orange colour at the base of the hind wing is very marked in some specimens and almost produces a basal triangle.

The form *striata* is extremely variable: on the one hand, in the male it passes through *theorini* into *ruhama*, (figs. 9 to 6, Plate I), while variations in the female produce other forms, one of which, shown at fig. 25, Plate III, seems sufficiently distinct to deserve a name, and is described below.

The specimens shown at figs. 23 and 24, Plate III, have the usual "ochraceous orange" modified into a paler colour, especially well shown in fig. 23, where there is a discal area of "warm buff" on the hind wing and a trace of a band of the same colour on the fore wing in areas 1*a*, 1*b*, and 2 on the disc. The underside shows a definite "ochraceous orange" basal triangle, with a distinct "warm buff" discal band.

The model for *striata* is *Bematistes vestalis* Felder.

(5) **stavelioides** forma nova.

The female shown at fig. 25, Plate III, is the type of this form. The basal half of each wing is yellow, corresponding with Ridgway's "deep chrome," which radiates almost to the margin of the front wing in areas 1*a*, 1*b*, and 2, and deeply into the border of the hind wing. The rest of each wing is "Vandyke brown." The under surface has the same pattern except for a basal triangle of "orange," but the general colour is paler.

This form corresponds beautifully to the form *stavelia* Suffert, of *Bematistes vestalis* Felder, as figured by Aurivillius (1912).

(6) *youbdonis* Ungemach, 1932.

Described from a unique male as having the base of each wing "brun orange vif," bordered by a diffuse area, narrow in the front wing, wider in the hind wing "d'un jaunâtre clair," beyond which the rest of the wing is of a uniform grey-brown.

The specimen figured on Plate III, fig. 22, seems to correspond fairly well with this description, save that the yellowish area beyond the basal orange brown (Ridgway's "cinnamon rufous") is rather indistinct. The dusky peripheral area of the underside is paler than above: the "cinnamon rufous" at the base of the hind wing makes a distinct basal triangle.

This form is obviously derived from *striata*, and a number of West African specimens have been seen which link *striata* with it, they have the "cinnamon rufous" area of the hind wing rather more extensive, and not bordered by the yellowish suffusion of *youbdonis*.

(7) *theorini* Aurivillius, 1898.

This form seems to be, in the male, a transition from *ruhama* to *striata*, with a quite small subapical yellowish band in areas 3 and 4 and no definite inner marginal pale area (see Plate I, figs. 8 and 9).

The female has a larger subapical band, of 3–5 mm. width: the specimens shown at figs. 43 and 44, Plate V, seem to agree with the description. The base of the hind wing below is "cinnamon rufous" but merges gradually into the brown distal area, so that there cannot be said to be a basal triangle. These two specimens, through that shown at fig. 42, grade into fig. 41, with an unusually large subapical band, and brown inner-marginal area on the front wing which thus links *theorini* with *consanguinea*. The aberrations *epigeoides* and *obtusedentata* of Strand (1914) may be individual variations.

Fruhstorfer's *karschi* (1903) seems to belong to *theorini*, but I agree with Aurivillius (1925) that the description is inadequate.

(8) *epigea* Butler, 1874.

This is a female form, but Butler's description is so muddled that it gives no clear definition. However, the type is available, and the specimen shown at fig. 30, Plate III, agrees with it.

As Butler points out it is somewhat like the male *eurytus* in colour and pattern. The pale areas are "ochraceous orange." Points to notice are: (1) The shape of the inner-marginal area of the front wing, which does not enter the bases of areas 1*a*, 1*b*, and 2; (2) the rather wide, and very dyslegnic, dusky border of the hind wing; (3) the underside of the hind wing has a basal triangle of "orange" (developed to different degrees in other specimens) bordered in areas 6 and 7 by a paler yellowish zone. These features distinguish *epigea* from its somewhat similar derivative *terra*. It seems, from fig. 29, that *epigea* may have been derived from the female of *ruhāma*: like the latter, it is a large form.

Specimens occur with the same pattern, but with the pale areas of a lighter shade, especially on the front wing, Ridgway's "warm buff," as shown at fig. 31, Plate IV. By means of such a specimen as is figured at fig. 32 we get a transition to the female of *fulvaria*, fig. 33.

(9) *fulvaria* Butler, 1874.

Described from the male as having a " broad strongly angulated tawny band, widening from subcostal nervure to inner margin " on the front wing, and the hind wings " with central area tawny ochreous from subcostal nerve to inner margin, deeper at base." A specimen corresponding with the type is shown at fig. 12, Plate II. The angular band is " ochraceous orange," as also the base of the hind wing, but there is a slightly paler suffusion between this and the " Vandyke brown " broad border. On the under surface the basal triangle is " ochraceous tawny," and better defined, and the pale suffusion makes a whitish band : the front wing is the same as on the upper surface.

Fulvaria is an extremely variable form in the shape of the angular band. Eltringham (1910) figures a specimen which, as he says, is not typical: it would fit in as an intermediate between *ruhama* and the specimen shown as fig. 11, Plate II. A specimen in the British Museum (Natural History) has the front wing band greatly reduced anteriorly so that it is barely shown in front of vein 3, there being only a rudiment at the base of area 4, and another at the end of the cell.

The female *fulvaria* was described as having on the front wing " an oblique broad creamy band from costal nervure to just below the second median where it becomes obsolete but is represented by a greyish nebula on centre of first median branch and reappears as a creamy ochraceous patch on inner margin." The hind wings have a black-spotted greyish ochraceous base and a central diffused creamy band from costa to inner margin, which is ochreous. On the underside " H.W. basal area bright tawny with black spots as in male." Fig. 33, Plate IV, shows a typical specimen : fig. 32 is transitional to it from *epigea*, and fig. 34 shows transition to *simulator*.

The basal part of the hind wing, and the inner-marginal area of the front wing are " warm buff." There is no trace of a basal triangle on the upper surface, but it is present below, of " ochraceous tawny " colour as in the male.

The form *fulvaria* was described as mimicking the two sexes of *Bematistes formosa* Butler, but as Eltringham (1910) pointed out, this is an error, for *formosa* has a narrow white discal band on the hind wing. Eltringham suggested that the male *Bematistes consanguinea* Aurivillius, would be a better model for the male *fulvaria*. As regards the female, Jordan (1911) figured a number of *Bematistes* of approximately the appearance of *fulvaria*.

(10) *simulator* Butler, 1873.

The description of *simulator* from a female, omitting unessential details was as follows : " F.W. with basal area blackish . . . ; a broad white band nearly equal in width throughout . . . crosses the centre of the wing obliquely from costal nervure to below centre of first median interspace ; three white rays on inner margin. H.W. with base tawny . . . ; a broad externally diffused white band crosses the wing from inner margin to costal nervure, and is about twice as broad at its lower as at its upper extremity . . ."

A female corresponding fairly well with the type is shown at fig. 35, Plate IV : the posterior part of the white band of the hind wing is a little masked by " ochraceous tawny." The basal triangle is well shown above and is still larger below, it is " ochraceous tawny." The general ground colour of the upper side is slightly blacker than the " Vandyke brown " hitherto considered and corresponds with Ridgway's " bone brown." The female *simulator* differs from *fulvaria*, with which it is closely connected by intermediates, by reduction of the posterior part of the pale bar of the front wing and by whitening of the discal pale area of the hind wings. There is also greater development of the basal triangle. (See fig. 33, Plate IV). Butler noted *simulator* as "A remarkable mimic of *Acraea* (*Planema*) *Euritea* ♀." Those interested to know what species he meant will find the Synonymic Table a guide: it was probably *macaria* F. which at that date included *macarista* Sharpe.

The male *simulator* is shown as fig. 15, Plate II: it is obviously linked with *fulvaria* (fig. 12), through specimens shown as figs. 14 and 13, by clarification and condensation of the whitish scales on the disc of the hind wing into a definite but narrow white band. The "ochraceous orange" band on the front wing is more sharply elbowed in area 3 than in *fulvaria*. There is a conspicuously large "ochraceous tawny" basal triangle on the upper surface, even larger below, where it covers all the cell and extends beyond the middle of the costa.

An atypical *simulator* is figured by Aurivillius (1912). The model for this form may well be *Bematistes excisa* Butler. The name *simulator* was wrongly used by Grose Smith (1889) for specimens from the East African coast quite different from Butler's: they are of the form described as *rogersi* by Trimen (1908). The "*togoensis*" of Bartel (1905) appears to belong to *simulator*: the form *tirikensis* to which Aurivillius assigned it (1912) is not known from West Africa, except the extreme eastern fringe of the Belgian Congo. Grünberg (1910) figures what he thinks is Bartels *togoensis*, but the figure and description correspond with a form of *tirikensis* with the basal triangle reddish (*vide infra*), whereas Bartel's *togoensis* = *simulator*.

(11) *hobleyi* Neave, 1904.

The original description of this male form compared it with *künowi* Dewitz, figured by Eltringham (1910), but that is a different species from *eurytus*, easily distinguished by having only one inter-nervular ray in area 1*c* of the hind wing, and the different shape of the front wing band; this in *hobleyi* is much broader anteriorly than in *simulator* with which it may well be compared, and from which *hobleyi* is probably derived (see Plate II, fig. 17).

Coloured figures of *hobleyi* were given by Eltringham (1910), Punnett (1915) and Carpenter (1920*a* and *b*). Uncoloured by Neave, 1906, Carpenter (1914, 1924, 1930), by Grünberg (1910) as "*togoensis*," and Tenniel Evans (1946). The white band on the hind wing is much wider than in *simulator* and is pure white throughout. There is a small basal triangle on the upper surface of the hind wing, in shade different from that of *simulator*, being "Kaiser brown." The triangle is very much larger on the under surface, though not quite so large as in *simulator*: the "Kaiser brown" colour lacks the suffusion with darker scales which obscures the true colour on the upper surface.

This form is normally confined to the male sex: Neave (1904) alluded to a female "of this species" differing "in slightly larger size and in greater width of orange bar of fore wing." This is now known as *poggeoides* Poulton (*vide infra*). Very rarely a female specimen is found in which the pattern and coloration of the bar across the front wing is that of *hobleyi*. This is produced chiefly by the distal outline of the basal black of the front wing which in *poggeoides* cuts through the tip of the cell, running through the two distal black spots. Thus the end of the cell is orange, reproducing the pattern of *tirikensis*, but with white replaced by orange (see text-fig. 28A). In *hobleyi*, however, the edge of the black does not join the two distal spots in the cell, but runs from the outermost more directly forwards to the costa, so that the basal black occupies most, or all, of the apex of the cell. Specimens of *hobleyi*, however, show variability in this character, even in the same locality, and also in the breadth and depth of colour of the band. Some might even be called male *poggeoides*, but the gradations are so small that it is difficult to separate them into two categories as either *hobleyi* or male *poggeoides*. On the other hand, female specimens with *hobleyi* pattern are apparently very rare, and better defined. I have only seen two specimens, one, in the collection of Mr. T. H. E. Jackson, from Kakamega, Kenya Colony; the other from almost the same locality (Ilala, near Mumias) in the National Collection (see text-fig. 28B).

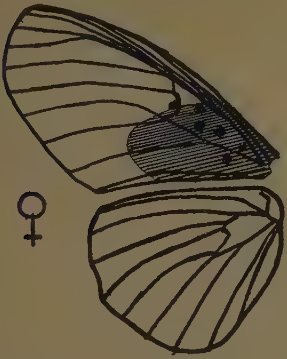


FIG. 28A.—*Pseudacraea eurytus poggeoides.*

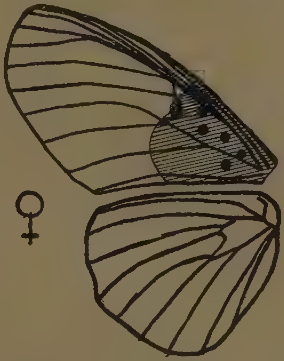


FIG. 28B.—*Pseudacraea eurytus hobleyi.*

Eltringham (1910) noted that *hobleyi* was the "eastern representative" of *simulator*: Plate II shows that it can be derived from *simulator* just as the latter can be derived from *fulvaria*. The chief difference is the anterior widening of the band on the front wing, the development of the white hind wing band, and a change in the tint of the basal triangle.

This form is fairly stable: variations are in the shape of the anterior portion of the front wing band, and the development of yellow on the hind wing band, leading to *hemixantha* and *opisthoxantha*. The model is *Bematistes macarista macarista* Sharpe, and the mimicry is perhaps one of the best among all the forms of *eurytus*. A form of *macarista* having the anterior portion of the bar of the hind wing yellow instead of white was described as *macarista rileyi* by Le Doux (1937). This is appropriately mimicked by an undescribed variation of *hobleyi*, to which I now give the following name:

(12) **hemixantha** forma nova.

As *hobleyi*, except that the anterior part of the bar across the hind wing is of the same colour as the bar on the front wing, as shown in fig. 19, Plate II, which is the type specimen. The amount of "ochraceous orange" on the hind wing may be less than in the type or may increase to the degree seen in the next form.

(13) *opisthoxantha* Carpenter, 1924.

The whole of the band on the hind wing is of the same "ochraceous orange" as that of the front wing. See Plate II, fig. 20. It is also figured by Carpenter (1924). This form, in other respects, is like *hobleyi*: it was first mentioned by Poulton (1911, p. 497) as an occasional aberration of *hobleyi*, but recent investigations (*vide infra*), show that it plays an important part in some areas. The model in Western Uganda may be *Bematistes pseudeuryta* G. and S., but this is not common and the inter-relation requires more investigation. In Eastern Uganda, the model is *B. aganice ugandae* van Someren.

Casual comparison of figs. 11 and 20, Plate II, might query the justification for separate names. It may be pointed out that fig. 11 represents a Western specimen, derived from *fulvaria* and *ruhama*, as shown by the shape of the narrow front wing band, the absence of a basal triangle above, and the "ochraceous tawny" large triangle below. On the other hand *opisthoxantha* has the broad front wing band of *hobleyi*, and, like that form, shows a "Kaiser brown" basal triangle above, and a larger one of the same shade below.

(14) **infumata** forma nova.

This is another derivative of *hobleyi*, having the dusky border of the hind wing much widened so that it greatly narrows the white band. In addition, what is left of the band is strongly suffused with yellow anteriorly, so that there is only left a narrow white area from the end of the cell to the anal margin. The replacement of white is less marked on the under surface. The type specimen is shown on Plate II, fig. 18.

(15) *künowoides* Carpenter, 1930.

Differs from *hobleyi* by the sharply elbowed front wing band, which is much narrowed anteriorly: its colour also is darker, being "ochraceous tawny" rather than "ochraceous orange." The large hind wing band is pure white as in *hobleyi*. At the anal angle of the hind wing there is a small suffusion with orange. This form is shown at fig. 16, Plate II, and comparison with figs. 12 and 15 shows that the darker, narrower, and more angular band comes from the *fulvaria-simulator* pattern. But the small dark basal triangle on the upper side is like that of *hobleyi* rather than *simulator*: on the underside it is also that of *hobleyi* in colour. These characters detract from resemblance to *Bematistes macarista*, the model for *hobleyi*, but as I showed in 1930, give *künowoides* a resemblance to a form of the quite different species *Pseudacraea gottbergi*. The nomino-typical *gottbergi* Dewitz, has a narrow brownish orange band on the front wing and one of the same colour on the hind wing, and mimics *Bematistes elongata* Butler, male. A form *künowi*, originally described as a distinct species, occurs in the eastern Congo, with a narrow white band on the hind wing; this, in Uganda, is much wider in the form *neumanni* Thurau (Carpenter, 1930), and it is this form which *künowoides* resembles. This is discussed later.

(16) *tirikensis* Neave, 1904.

This form is closely linked with *hobleyi*, and the following quotation from Eltringham (1910) is given "*P. hobleyi* presents a very interesting case of sexual dimorphism. The female was first described from three examples, two of which were at first thought to be males, and the species was named *tirikensis*. A further examination, however, assisted by the acquisition of more material, showed that the form *tirikensis* was always female, and further that *hobleyi* was always male. As the two forms always occur together, there can be little doubt that they are the sexes of one species for which the name *hobleyi*, originally given to the male form, must stand." Proof of this was furnished by synepigonic families (Poulton 1912, 1913*a*).

Neave's description and figure shows that typical *tirikensis* has an oblique subapical white bar cut off from a very small inner-marginal area on the front wing, hardly more than the "three white rays" mentioned in Butler's description of *simulator*. There is a broad dark border to the hind wing, and (on the upper surface) a basal area of the same "bone brown" colour as the rest of the dark parts: the median white band is rather narrow. On the under surface the basal triangle is large, extending half way into the cell and half way along the costa: it is of the same "Kaiser brown" colour as in *hobleyi*.

A typical specimen is shown on Plate IV, fig. 38: other figures are given by Eltringham (1910), Punnett (1915), Carpenter (1920*a*, *b*), in colours: uncoloured figures by Carpenter (1914, 1924, 1930), and Tenniel Evans (1946). The transition from *simulator* to *tirikensis* is very easy, and well exemplified by a West African specimen recorded as *hobleyi* ♀ by Holland (1920), which Dr. Michener kindly sent to me to study: it came from Belgain Congo, Medje, 27° 15′ E., 2° 25′ N. The fore wing is almost that of typical *tirikensis*, but the inner-marginal white patch is smaller and more duskily suffused.

Another specimen, also kindly lent by Dr. Michener, from Gold Coast, Huni Valley, has a complete white band on the fore wing, as in fig. 39, Plate IV. Both these western specimens, however, reveal themselves as *simulator* by the red-brown colour (Ridgway's "ochraceous tawny") of the basal triangle above and below, whereas in typical *tirikensis* it is blackish above and "Kaiser brown" below. The usual tawny colour of the anal part of the hind wing of *simulator* is reduced, in the Medje specimen, to a trace at the anal angle only, and cannot be seen in the Gold Coast specimen.

The form *tirikensis* shows interesting variations, departing in three directions from the type: (A) The white marks on the inner margin of the front wing are only suggested by the faintest possible suffusion with white, as in fig. 37, (cp. fig. 36). (B) They are so much increased that there is a broad continuous white band with faint dark streaks across it in areas 1*a*, 1*b*, as in fig. 39. (C) The basal triangle shows distinctly a reddish shade on the *upper* surface, as in fig. 39, (and in Eltringham's figure). Variation A produces much greater resemblance to the model, *Bematistes macarista* Sharpe, female: indeed, as with *hobleyi*, the mimicry is about the best among forms of *eurytus*.

Variation B detracts from likeness to the chief model, but reference to Jordan's figures (1911) shows likeness to others.

Variation C is particularly interesting as evidence of the derivation of *tirikensis* from *simulator*, in which the basal triangle is very conspicuously reddish above (Plate IV, figs. 35–36).

Reference must be made here to a coloured figure by Jones (1785) of a peculiar aberration, un-named by him, and said to be in the Francillon collection. It is reproduced now as figs. D1, D2. It seems unlikely that the specimen should have come from the haunts of *tirikensis*, which were not collecting places for butterflies at that time. Yet I have seen no specimen from West Africa resembling this one, which is certainly nearest to *tirikensis* and probably a form of *simulator*. It was not named by Jones. It will be noted that the figure of the under surface shows a pattern on the front wing like that of fig. 39 on Plate IV.

(17) *poggeoides* Poulton, 1913.

This is an interesting female form, first mentioned by Neave (1904) and Poulton (1911, p. 496) as a female of *hobleyi*, with the colouring of the male. It is shown as fig. 40, Plate IV. It has also been figured in colour by Carpenter (1920*a* and *b*, and 1924 uncoloured). The name *poggeoides* was applied by Poulton to "female forms with the pattern of *tirikensis*, but a fore wing colouring approximating to that of *hobleyi*. It would probably be found when a long series was examined, that the orange bar of *poggeoides* was paler than that of *hobleyi*, just as *poggei nelsoni* was, in this respect, paler than *macarista* ♂."

The long series is now available and establishes this point: the colour of the front wing band corresponds to Ridgway's "antimony yellow." It will be noted that the form of the band is that of *tirikensis*, and its posterior end varies as in that form: a unique specimen shown at fig. 58, Plate VI, corresponds to the *tirikensis* shown at fig. 38, Plate IV, whereas the typical *poggeoides* is nearer fig. 39. The band in *poggeoides* is more oblique anteriorly, and has a more angular outline in area 2 than in typical *hobleyi*. The differences in the band of *poggeoides* and *hobleyi*, and their respective models, can be seen in the coloured plates under the references Carpenter 1920*a* and *b*, and the uncoloured in Carpenter, 1914 and 1924. The model for *poggeoides* (*Bematistes poggei nelsoni* Grose Smith), is also figured by Eltringham (1910): it is monomorphic, so that here we have a female form of *eurytus* mimicking male as well as female of its model. (*N.B.*—See previous remarks on " male *poggeoides* " under *hobleyi*.)

Since writing the general account I have recently (January, 1949) had the privilege of seeing the fine collection of Mr. T. H. E. Jackson at Kitale, Kenya Colony, and discussing with him these yellow and white forms. It is clear that there are males and females of both *hobleyi* and *poggeoides*, the usual sex for *hobleyi* being male, and female for *poggeoides*. The difference, shown by figs. 17 and 40, lies in the shape and colour of the band on the fore wing. In *hobleyi* the outer margin of the basal black makes a rounded curve rather than a definite angle and there is only a minute triangle, at the end of the cell, of the *orange* band. In *poggeoides* the black base is sharply angled so that the edge meets the costa nearer the base of the wing, leaving a larger, *yellow* triangle at the end of the cell. The shape of the black basal area is that of a *tirikensis*, in which the white band reaches maximal development (fig. 39); as Poulton originally pointed out, *poggeoides* is *tirikensis* with the fore wing band yellow instead of white. In female *hobleyi* the shape is that of the male *hobleyi*, and the colour is the same orange. As in other forms of *eurytus* in Uganda and East Africa there is considerable variability, but typical *hobleyi* are clearly separable from typical *poggeoides* in both sexes. Mr. Jackson has taken male *poggeoides* in the forests on the west coast of Lake Victoria; the females have been found in Lotti forest on the Acholi mountains of the Southern Sudan, in Budongo and Kalinzu forests of western Uganda, in the forests round Entebbe and on the Sese islands, and in the eastern province of Uganda. The form is proportionately commoner to the east, and the only captures by Mr. Jackson in the forests of Kakamega, Kenya Colony, to the east of Lake Victoria, have been of this form where he has also taken a female *hobleyi*. The predominance of the yellow or orange banded females in this locality is in accord with the absence of a black and white female of *Bematistes*.

(18) *mimo-ras* Ungemach, 1932.

Figured in colour by Ungemach: I have not studied a specimen. There is an oblique orange band across the front wing just beyond the cell with a greyish discal area on the hind wing. The female has the orange band brighter and larger, but not going beyond vein 2: there is also a narrow dusky white inner-marginal area. The hind wing in the male has a grey area replacing the white band, which occupies most of the wing in the female, except for a deep brown basal triangle.

On the under surface in both sexes there is a red-brown basal triangle. This fine form mimics *Bematistes poggei ras* Ungemach, figured by Ungemach (1932).

(19) *lachesis* Ungemach, 1932.

Described and figured from two females. The front wing has a rather oblique, triangular, white band, wider on the costa and reaching very nearly to the margin along vein 3: there is a small inner-marginal whitish area crossed with black streaks. The hind wing is as in *mimo-ras*, with a white discal area, but between this and the black border there is a grey band 3 mm. wide.

(20) *epaeoïdes* Ungemach, 1932.

Described and figured from one female as differing from *eurytus* in the following points. The pale areas are " jaune d'ocre pale." The oblique subapical band is wider, does not touch the cell and reaches the costal margin along all its width of 6 mm. The inner-marginal area extends to 7 mm. from the outer margin, and along the posterior margin of the cell as far as the root of vein 3, and along that vein for half its length. The black border of the hind wing is narrower than in *eurytus*. On the under surface there is no basal triangle, but " les bases des intervalles 7 et 8 de l'aile post, sont orange." This form seems to have some affinity with the following.

(21) *terra* Neave, 1904.

Described as " dusky brown, heavily marked with dull ochraceous yellow," and allied to *eurytus*, by which is meant that the front wing has subapical and inner-marginal areas completely separated. The inner-marginal area is large and, as in *eurytus* male (but not female), occupies the base of area 2, and often the extreme base of areas 1*a*, 1*b*. This differentiates *terra* from *epigea* : another point of difference is that *terra* has on the under side of the hind wing, neither the basal darker triangle nor the paler zone distal to it possessed by *epigea* : there is only a very small area of darker orange anterior to vein 8. The pale areas are " ochraceous orange." Both sexes are alike ; a female is shown as fig. 48, Plate V. Generally speaking this is a very stable form, wonderfully mimicking *Bematistes tellus eumelis* Jordan, which is figured by Eltringham (1910). Other illustrations of *terra* are to be found in Eltringham (1910), Punnett (1915), Carpenter (1920 *a*, and *b*) in colours ; uncoloured figures are given by Carpenter (1914) and Tenniel Evans (1946).

Variation is shown, especially on the Sese Islands (Carpenter, 1914), in the black bar separating the two areas on the front wing, as shown by figs. 49 and 50, Plate V : the latter seems to be the " ab. *impleta* " of Grünberg (1910, fig. 7). This specimen is an obvious intermediate between *terra* and *tirikensis*, for on the under surface it has a well defined basal triangle, and the band on the front wing is almost white anteriorly. Intermediates between male *terra* and *hobleyi* can also be distinguished by the development of a basal triangle and, often, a whitish band distal to it on the under surface.

Variation in colour, but not in pattern, by dark suffusion of the orange areas, connects *terra* with the form next to be described.

(22) *obscura* Neave, 1904.

Described as " dusky brown dusted with lighter brown." The pattern is as in *terra*, but the pale areas, of slightly lighter colour than in *terra*, are dusted with scales of the general ground colour, which is of a greyer brown than the " Vandyke brown " usual in forms of *eurytus* and corresponds with Ridgway's " Saccardo's umber." The type specimen shows no definite basal triangle: this, however, is developed to a certain extent in some specimens, but of a paler tint than in *hobleyi* or *tirikensis*. The female was described as paler than the male.

This form is figured on Plate V, fig. 47 : a previous coloured figure was given by Carpenter (1920*a*, *b*). The form figured as *obscura* by Tenniel Evans (1946), will now be known as *jacksoni* Crpntr., his "*imitator*" shows a specimen agreeing with *obscura*. There is no very apt model, but in proportion as *obscura* grades into the form next to be described it resembles the Uganda race *paragea* Smith and Kirby of *Bematistes epaea*, figured by Eltringham (1910). Neave's *obscura* is a stage in transition from *terra* to the form next to be described, and grades very finely into *terra*, so that few specimens are quite alike.

(23) **grisea** forma nova.

This has usually been discussed under *obscura*, but the time has come for it to be distinghished. Male and female are much alike, save that, as in *obscura*, the female is somewhat paler.

Ground colour lighter than usual in forms of *eurytus*, of a greyish brown, corresponding with Ridgway's "Saccardo's umber." The front wing has an oblique pale yellowish ("light buff") subapical bar, well beyond the end of the cell, not quite reaching the costa and extending posteriorly to the inter-neural streak in area 3. There is diffuse dusting with "light buff" in areas 1*a*, 1*b*, just extending across vein 2 into area 3. The hind wing has the margin of "Saccardo's umber" but almost immediately, internally, it becomes suffused with "light buff" progressively more towards the base, which is of the same tint as the subapical area.

The under surface is much the same except for a small basal triangle of yellowish brown corresponding with Ridgway's "mars yellow": this hardly enters the cell and does not extend half way along the costa. The type, a female, is figured on Plate V, fig. 46. This form goes with *Bematistes epaea paragea* Smith and Kirby: it is, however, variable, and specimens much darker than the type match dark specimens of *paragea*, such as Eltringham figures (1910). Form *grisea* is also figured by Carpenter (1914, though the specimens often grade into *obscura*).

A remarkable specimen is shown at fig. 45, Plate V, in which the pale areas have become almost wholly suffused with the general ground colour, except for a small and indistinct subapical bar. The ground colour is browner than in *grisea* and *obscura*, of the tint "snuff brown." Such a specimen as this perhaps led Aurivillius (1925) to discuss *obscura* as a form of *theorini*.

(24) **jacksoni** forma nova.

This is a localized form, obviously closely related to *obscura* and *grisea*, but with the pale areas contracted and more sharply defined. Male and female are similar.

The ground colour is Ridgway's "Vandyke brown." The front wing has a very small oblique area at the base of area 4, extending into part of the base of area 5, of Ridgway's "ochraceous buff," and a faint suffusion with this colour extends into area 3. A small area of the same colour occupies the middle of areas 1*a* and 1*b*, extending forward into area 2, but not into its extreme base. The hind wing is mainly "Vandyke brown" but the anterior half of the cell and the base of areas 6 and 7 are "ochraceous buff." The under surface shows the buff areas slightly larger; the oblique bar on the front wing extending to the outer margin at the end of vein 3, and the greater part of the cell of the hind wing being pale. The anterior margin of the cell and the base of the hind wing in front of it define an area of "mars yellow" which is quandrangular rather than triangular as it extends very little outwards on the costa. The type male is shown at fig. 70, Plate VII. A figure of a specimen of this form is given by Tenniel Evans (1946) as *obscura*. This distinct form is a very close mimic of a corresponding form of *Bematistes epaea*, in the same localities.

(25) *bicolor* Aurivillius, 1898.

An extremely beautiful form with the subapical area brilliant shining white in the female: the other pale areas of a very rich golden orange, corresponding with Ridgway's "zinc orange."

The ground colour of the female is blacker than usual, even darker than the "bone brown" of *tirikensis*, and matches Ridgway's "aniline black." The narrow border of that colour on the hind wing is sharply defined. There is no basal triangle, even underneath. The male has the subapical bar much reduced, and only a little paler than the inner-marginal " zinc orange " : on the under surface it is almost white. In the female the subapical area is almost rectangular, and broader in proportion to its length than in *terra* : it is nearly as wide in proportion as in *epigea*. This form is discussed by Grünberg (1910, p. 168).

The female is shown as fig. 59, Plate VI, and the male as fig. 60. This form was figured under the name " *schubotzoides* " by myself (Carpenter, 1935), and by Tenniel Evans (1946) : this name must sink as a homonym.

The model is *Bematistes tellus schubotzi* Grünberg, figured in the last named reference.

(26) *ruwenzorica* Grünberg, 1912.

This highly remarkable form was described and figured from a single specimen, and no other has been recorded. A reproduction of the original figure is given in Carpenter, 1948. The ground colour is described as velvety black : the base of the front wings is suffused with brownish red extending from the inner margin to cover most of the cell but not extending outwards into area 3. The subapical band is broad and extends from the costa to just in front of vein 2 : in area 3 it is 9 mm. broad and almost reaches the outer margin, but in area 2 it is only 5·5 mm. broad and is thus angled. The band does not enter the bases of areas 2 and 3, nor the cell : it is bright ochre-yellow. The inner-marginal area, also bright ochre-yellow, is small and consists of two parts, that in area 1*a* measuring 6·5 mm. in width, that in area 1*b*, 4 mm., reaching to vein 2. It is remarkable, seeing that large collections have been made on Ruwenzori, that no other specimen is known. The model, *Bematistes quadricolor latifasciata* E. Sharpe is plentiful.

(27) *victoris* Eltringham, 1910.

Described and figured in colour, from a female : this is the only female I have been able to examine. The greater part of the front wing was described as sienna brown : the colour corresponds with Ridgway's " hazel." The apex and a bar running from the tornus to the origin of vein 5, are " bone brown " ; as also the broad border to the hind wing. A well-defined basal triangle on the hind wing of " madder brown " is somewhat suffused on the upper surface with dusky scales : it extends half way into the cell and a little more than half way along the costa. Between it and the dark border is a white discal band, much narrowed at the costa, and shading off externally into the dark border. The under surface is similar to the upper, but the basal triangle is brighter. Through the kindness of Mr. Saunders I have been able to see a male (figured in Carpenter, 1948*a*) captured by him in northern Kenya Colony, at Meru. The dark bar separating the subapical area is extremely ill-defined. The basal triangle on the underside of the hind wing is so much larger than in the female that it occupies about half of the wing. This indicates affinity with the east-coast form *rogersi*, which has the triangle considerably further extended outwards than in the Uganda *hobleyi* and *tirikensis*.

Victoris is a peculiar form and has a curious likeness to the form *albostriata* Lathy of the very distinct species *Pseudacraea dolomena* Hewitson. This depends largely upon the unusual tint of the front wing. The white-ringed spots along the anterior border of the cell in *dolomena* distinguish it : the basal triangle is also duskier on the upper side, and larger, in *dolomena*, while on the under surface in that species it is only faintly indicated as a greyish tint.

The form *victoris*, at least in the female, resembles *Bematistes quadricolor leptis* Jordan : the male, as so often is the case, is a less perfect mimic. The chief feature of the resemblance is the purplish tint of the brown, characteristic of the model and well copied by the mimic. It is, among other forms of *eurytus*, only shown by the last discussed *ruwenzorica*, a better mimic of the same species of *Bematistes*, in the form *latifasciata* E. M. Sharpe.

(28) *rogersi* Trimen, 1908.

Strongly sexually dimorphic. The male in Trimen's brief introductory description was described as " Fuscous, with yellowish rufous areas, with black basal and sub-basal spots, and black nervules and inter-nervular rays." It is shown in three forms on Plate VII, figs. 61, 62, 63, of which 62 is very near to the type which is figured in colour by Eltringham (1910) and Carpenter (1920*a* and *b*).

The ground colour is " Vandyke brown " but on the apical part of the front wing there is considerable suffusion with pale scales so that the dark veins and intervening rays produce a streaky effect, not seen in Eltringham's figure, but well shown by the artist in Carpenter (1920), and especially mentioned by Trimen. The dark border of the hind wing is narrow and unusually uniform in width. There is only a trace of basal triangle on the upper surface, indicated by faint dusky shading of the extreme anterior part of the cell and the proximal half of the costal margin. There is great variability of the dividing dark bar on the front wing: in the type it is much thinned towards the tornus, but does just connect with the dark border (not shown by Eltringham). On Plate VII, fig. 61 shows maximal development, fig. 62 slightly less than the type, and fig. 63 shows no trace of it. The pale area is of an almost pinkish orange, corresponding with Ridgway's " orange rufous." The under surface is much paler than the upper and the discal area of the hind wing of the specimen shown in fig. 63 is very nearly white.

There is a well developed " Kaiser brown " basal triangle, not extending more than half way into the cell, but along the costa almost reaching the tip of the wing. This form, owing to the peculiar tint of its pale colouring, has a curious resemblance to the distinct species *Pseudacraea dolomena dolomena* Hewitson. It is readily separated by not having the basal spots of the front wing surrounded by white rings, and by the presence of a basal triangle. Grose-Smith commented on this likeness. The female *rogersi* was thus shortly described by Trimen. "Fuscous ground darker than in male, almost black; fulvous markings of male replaced by pure white ones." The ground colour is " bone brown," the white areas consist of a large subapical bar and small inner marginal area on the front wing, and the greater part of the hind wing. The subapical area extends from the costa to the inter-nervular ray in area 2, and its general direction is slightly curved. The inner-marginal area is variable, its maximal development is shown in the specimen figured as 53, Plate VI, in which it extends across vein 2 into the base of area 2. In the type as in the specimen shown as fig. 52, the inner-marginal area does not reach area 2. As in the male there is only a faint trace of basal triangle on the upper surface, and this, combined with the narrow border of the hind wing, makes the wing much whiter than in any other form of *eurytus*. On the under surface the basal triangle is relatively smaller than in the male, but of the same " Kaiser brown ": it only extends half way along the costa and not half way into the cell.

The female allotype was illustrated by Eltringham (1910) and Carpenter (1920*a* and *b*). The model for the female is *Bematistes adrasta pancalis* Jordan, but the pattern and peculiar shade of the male make it a poor mimic. When first captured *rogersi* was described as mimicking the female of *Bematistes aganice montana* Butler: Trimen (*loc. cit.*) writes of " the likeness to *Pl. montana*, which has undoubtedly been gained by the quite peculiar position, curvature, prolongation, and inner indentation of the sub-apical bar." Since *aganice* is immensely commoner than *adrasta* it is very probable that it has more protective effect than the latter; but *adrasta* is more like the mimic.

(29) *conradti* Oberthür, 1893.

Described and figured from a male as resembling *eurytus eurytus*, but differing "par la forme et la disposition des bandes fauves . . . , en dessous . . . par la tache basilaire brun vineux à reflet violacé . . ." A male corresponding with Oberthür's figure is shown as fig. 67 on Plate VII. The rather dark ground colour is "bone brown," the pale areas "ochraceous tawny," and the basal triangle, not shown on the upper surface, is of the brownish-red called by Ridgway "Kaiser brown"; it is large, extending into the middle of the cell and along the costa to beyond the middle. The typical specimen shown at fig. 67 is not the commonest form of this interesting form of *eurytus*: the majority have the dark dividing bar on the front wing partly or completely broken through, so that the form figured at 64, Plate VII, results. By this change a beautiful mimetic resemblance to *Bematistes adrasta pancalis* Jordan is produced. The female of *conradti* has not been described previously.

Specimens from the same precise locality as the males provide the probable female of *conradti*, and one is shown as fig. 54, Plate VI. The dark ground colour is "bone brown": the subapical area is white, and the very small inner-marginal area is "orange buff." The sharply defined central pale area of the hind wings is "cream." The basal triangle reaches to the middle of the costa: on the upper surface it is "bone brown," on the under surface "Kaiser brown." The yellow tint on the front wing may slightly tinge the white subapical bar, or may be lessened so that this form is white-marked, or nearly so, and it may be hard to distinguish from *rogersi*. Comparison of figs. 52 and 53 with 54 shows that *rogersi* has a narrower border to the hind wing and no basal triangle on the upper surface: specimens with these characters do not show the yellowish tints of *conradti*. The model for these yellow-marked females, which are ascribed to *conradti*, may be *Acraea esebria* Hewitson (*fide* T. H. E. Jackson) and *Bematistes aganice aganice* Hewitson. Two females from Chinteche, Nyasaland, provide a link with *mlanjensis*. They have yellowish white hind wings and a small yellowish inner-marginal area on the fore wing. One, however, has the large white sub-apical area which characterizes *mlanjensis*, while in the other the sub-apical area is narrow, as in a *conradti* from Mrowi.

(30) *fickei* Weymer, 1907.

A male form described and figured from a single specimen: it seems to be only a variation from *conradti*, in which the pale area of the hind wing is white instead of the same orange colour as that of the front wing, and is diminished in size by a wider dark border.

Aurivillius (1912) describes as "*occidentalis*" a variation with the hind wing area yellow, from the Gold Coast. This locality seems highly unlikely, for there is considerable difference between western and eastern forms as will be shown later. Mr. F. Bryk kindly wrote from Stockholm Museum, in reply to enquiries, that the unique type specimen was supplied by Fruhstorfer. It has occurred with other material that Fruhstorfer's localities are sometimes erroneous, and this certainly is the case with "*occidentalis*," and the name is most regrettable. It should be abandoned, for it is clear from notes and a drawing kindly suppplied by Mr. Bryk that the specimen differs little from Weymer's figure except that the central area of the hind wing is yellowish ("soudern fahl hellederfarben"). I have figured on Plate VII, fig. 65, a specimen from Tanganyika Territory which agrees with Mr. Bryk's drawing of "*occidentalis*," and seems to be intermediate between it and *fickei* as the hind wing area is yellowish-white, paler than the front wing bar, but is white on the under surface as in *fickei*. This produces a certain resemblance to *hobleyi*, but the shape of the front wing band is different and the basal triangle differs in shade from that of *hobleyi*, as Mr. Bryk reports is also the case with "*occidentalis.*" The shade is slightly tinted with the "madder brown" of *victoris*. A series of these forms would probably show that *conradti*, *fickei* and "*occidentalis*" grade into one another.

(31) **pondo** forma nova.

The specimen shown at fig. 66, Plate VII, so far as I know is unique, but it has not the appearance of an individual aberration, and is therefore now described as a form.

The coloration is that of *conradti*, but the inner-marginal area of the front wing is greatly expanded, covering three-quarters of areas 1*a* and 1*b*, from their bases, and the base of area 2 in which area the "ochraceous orange" colour makes a triangular patch. The subapical bar is narrower than in *conradti*; the dark border of the hind wing much narrower, almost vanishing at the anal angle. The basal triangle on the under surface has a stronger purplish sheen than in *conradti*, corresponding with Ridgway's "madder brown"; it also extends further along the costa than in *conradti*, almost to the apex.

(32) *mlanjensis* Carpenter, 1920*a* (p. 98).

Described and figured from a series captured by S. A. Neave on Mt. Mlanje, Nyasaland. Shown on Plate VII, fig. 68, ♂; Plate VI, fig. 55, ♀. The male is comparable with male *conradti* (fig. 67) but the pale areas instead of "ochraceous tawny" are much lighter, corresponding with Ridgway's "pale orange yellow." The inner-marginal area on the front wing is much smaller than in *conradti*, and is only represented by a trace, and may be aborted. The colour of the basal triangle on the under surface is "Kaiser brown," as in *conradti*. The general ground colour is "bone brown."

The female *mlanjensis* shown on Plate VI, fig. 55, can be compared with *conradti* and *rogersi* above it. There is no tint of yellow in the pale areas, which are pure white: that on the inner margin of the front wing is as small as in *conradti* or smaller, so that it is hardly traceable, and therefore much smaller than in *rogersi*. The hind wing has a basal triangle on the upper surface of the same "bone brown" as the other dark parts, thus differing from *rogersi*: the dark border is, in width, between that of *rogersi* and *conradti*. The white subapical bar of the front wing, as in *rogersi*, crosses vein 2, whereas it does not in *conradti*.

The basal triangle on the under surface is "Kaiser brown." This form, in both sexes is an effective mimic of the form of *Bematistes aganice* occurring on the same mountain (Carpenter, 1920*a*, p. 98).

(33) *imitator* Trimen, 1873.

Described from two females, one of them "more decidedly tinged with yellow than the other." Trimen compared it with Hewitson's figures (1868) of "the typical form of the ♀ *Hirce* (*Eurytus*, Clerk) from Calabar," and for long it was the only other well known form of this species.

It differs from *mlanjensis*, just considered, by the reduced size of the pale areas, especially noticeable in the sub-apical area of the male. The basal triangle on the under surface has a slightly more purple sheen than in *mlanjensis*, corresponding to Ridgway's "liver brown": it is as large as in *mlanjensis*. In the male the pale areas are "pale orange yellow": in the female, usually white, but sometimes "cream"—a little paler than the male. The male is shown as fig. 69, Plate VII, the female as figs. 56 and 57, Plate VI. The female was figured by Trimen (1887), and in colour by Eltringham (1910), and Carpenter (1920*a* and *b*), gave coloured figures of both sexes.

It is interesting to note that Eltringham (1910), who had apparently not seen *conradti*, wrote: "Aurivillius [1898] includes *P. conradti*, Oberth., under this species; but *conradti* is evidently a very different form and has the paler markings brownish yellow. It appears to resemble the ♂ *P. eurytus*." But the forms discussed here, previously to *imitator* (Nos. 32, 31 and 29), show that Aurivillius had a clearly correct conception of the relationship which further specimens have demonstrated.

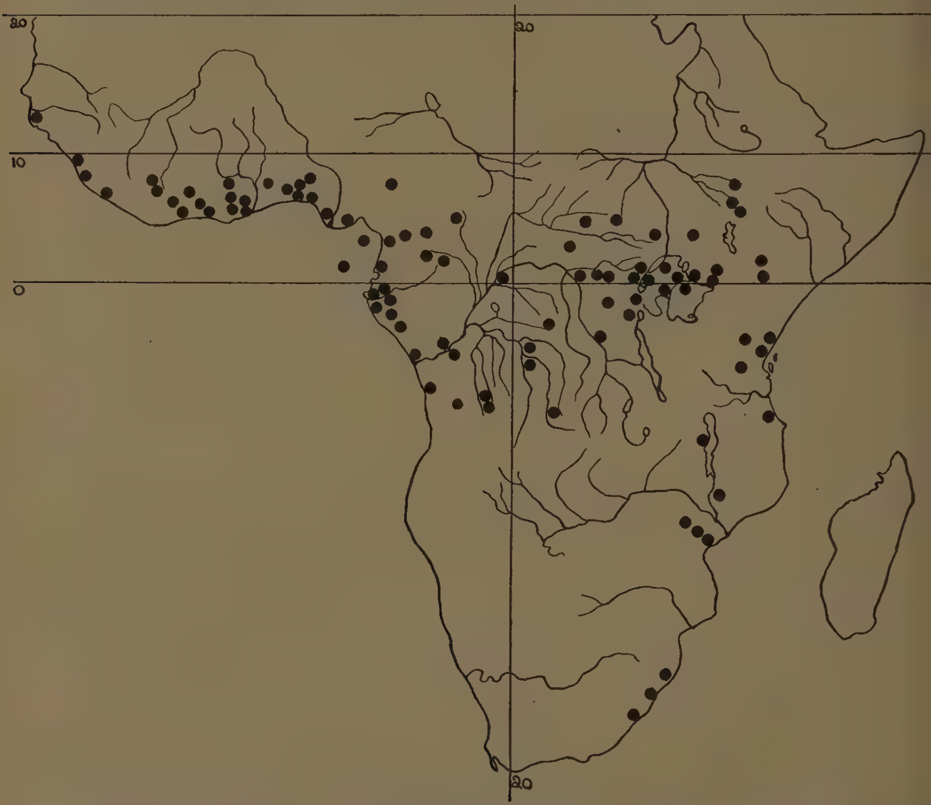
The form *imitator* was noted in Trimen (1873 and 1887) as a close mimic of *Bematistes aganice aganice* Hewitson. It is noteworthy that the yellow variant of the female mimics the male, which is unusual, while the white form mimics the white female of the model.

With the form *imitator* the list closes; the question, however, arises whether these are all of equal rank and whether some may not justly be termed subspecies. It is quite impossible without much more information based on large collections from precise localities, in the case of West African forms, to say that they are anything more than forms, except the very remarkable and apparently isolated *ruwenzorica*, of which only the type specimen is known: it may well be a subspecies. The several forms flying intermingled in Uganda must be looked upon as a closely interbreeding community none of which have attained sufficient isolation to become subspecies.

In Abyssinia the named forms seem to have become distinct enough to deserve the rank of subspecies: indeed, from their isolation they may have attained specific rank. Yet such a form as *youbdonis* (No. 6) is well linked up with *striata* (No. 4), and further knowledge of south western Abyssinian fauna may link the other forms with these along the Sudan-Uganda border, or on the Congo-Nile divide. An allusion to *Papilio dardanus* is apt. The males in south-west Abyssinia, like those in other parts of that country, have genitalia of the eastern and southern type. But on the mountains of the Sudan-Uganda border they have the western type of genitalia (Carpenter, 1948*b*) In the case of *eurytus* the transition from Uganda to Kenya and the south-east is not well shown. Between the eastern-most Uganda form (*poggeoides*, No. 17) at Kakamega in Kavirondo and the nearest eastern form *victoris* (No. 27) from Mt. Marsabit, there is a gap of at least 150 miles, and there is little similarity between the two forms. I have no records of any form of *eurytus* from Mt. Kenya, which is very surprising, but the butterfly fauna of that mountain has not been well investigated. The form *victoris* will probably be found to grade into the coastal *rogersi* (No. 28), and thence there is an easy transition down the east side of Africa into *imitator* of Natal (No. 33). At one time the last-named seemed to be a "good species," but the discovery of the remarkable form which is now named *pondo* (No. 31) links *imitator* easily with the Nyasaland form *mlanjensis* (No. 32), and *conradti* of Tanganyika Territory (No. 29).

VII. Distribution of Each Form.

The *map* records the distribution of the whole complex of *eurytus* compiled from specimens, published records, and letters from correspondents. It will be noted that there is no evidence of the existence of *eurytus* in any form on the Zambesi system except for a tiny intrusion from the coast along the railway from Beira. It is evident that there has been a barrier to the spread of the species beyond the head waters of the Congo system, from West Africa. Its origin in West, rather than East Africa is borne out by its occurrence on the islands of the Gulf of Guinea, but not on Zanzibar or Pemba. Nor does it occur on Madagascar, although the genus is represented there by the peculiar species *glaucina* Guenée and the form *apaturoides* Felder of *lucretia* Cramer, of which species another form, *comorana* Oberthür, occurs on the Comoro Islands.



Distribution of *Ps. eurytus*. A dot indicates record of one or more captures, but gives no indication of abundance.

I have sought information as to whether these peculiarities of distribution find any parallel in plants and birds, and append statements received through the kindness of correspondents.

(A) From Mr. J. P. M. Brennan, of the West African Forestry Service, July, 1947 :

" The main area of tropical and equatorial forest in Africa lies in the west, extending eastwards to Uganda and the Bukoba region of Tanganyika Territory. Small patches of rain-forest occur in the neighbourhood of some of the higher mountains of East Africa, e.g. Usambara in Tanganyika Territory, and nearly all the higher hills and mountains carry more or less extensive areas of montane rain forest. The genera represented in these forests are often similar to those of West Africa, but the species are normally different. The savannah regions carry a very distinctive flora, usually with little relationship to that of the rain forest, although in certain areas, notably Northern Rhodesia, xeromorphic species of genera otherwise inhabiting wetter regions occur, e.g. *Sapium*, *Chitandra*, etc., suggesting that at a more or less remote time these areas had a wetter climate.

" The coastal belt from southern Kenya southwards is often occupied by a richer vegetation than that of the savannah areas. This reaches its highest development in local areas of evergreen forest. In the vegetation of the coastal strip several West African genera are represented by usually very distinct species, e.g. *Cistanthera*, *Cola*, *Mansonia* ; the endemic species are numerous, and the vegetation gives the impression of being a specialized and rather depauperate derivative of a type formerly living under a higher rainfall, and showing certain affinities with the montane forests of Nyasaland and south-west Tanganyika Territory.

" A predominance of tropical genera extends down the east side of Africa to Natal, where an endemic species of such a typically tropical genus as *Cola* occurs. Certainly much of the coastal vegetation of east and south-east tropical Africa seems to point to major climatic changes in the relatively recent past."

(B) From Mr. R. E. Moreau, the well-known ornithologist, 17th September, 1947 :

" I cannot at the present time think of any birds that have a distribution like that of your *Pseudacraea*. What is its habitat ? I should guess from the distribution of evergreen growth in the lowland zone, probably gallery forest and secondary forest rather than primary forest. If this is correct I do not think that the ' right ' habitat would be at all well distributed in Southern Rhodesia, but there is quite a bit of it in Nyasaland and some in Northern Rhodesia, especially in the extreme north and north-west. There are, of course, a good many cases of West African birds that do not cross the Nile-Congo or the Rhodesia-Angola watershed, but I know of none of these which reappear on the eastern seaboard as your *Pseudacraea* does."

(C) From Mr. C. M. N. White, of the Northern Rhodesian Administration, an ornithologist of experience in the Mwinilunga area, 10th September, 1947 :

" The Congo-Zambesi water-parting is characterized by a very small degree of orographical definition. Along the border of the Katanga and the Mwinilunga border of Northern Rhodesia the summit of the watershed is only about a hundred feet higher than the surrounding country. The bird population of the northern part, Mwinilunga and the Katanga, is therefore more or less identical and extends westwards into Angola with only small changes.

" The Zambesi-Angola water-parting is a more pronounced barrier which often has a marked zoo-geographical significance although, orographically, in Balovale and Angola it is no more marked than the Congo-Zambezi water-parting.

" Quite a number of western and north-western birds seem to keep to the west of the Zambesi here, such as *Francolinus coqui angolensis*, *F. albogularis meinertzhageni*, *Mirafra africana kabalii*, *Eremomela griseoflava salvadorii*, *Telophorus viridis vieirae*, which belong to the fauna of the lower Congo and western Angola, and just enter Rhodesia on the west side of the Zambesi in Balovale district. *Prima flavicans*, which ranges from Ngamiland to the highlands of Angola, and *Mirafra africanoides tsapnelli*, which is characteristic of Bechuanaland, also only occur on the west of the Zambesi in Northern Rhodesia, although they have a southern origin."

I have had no experience of the primary forests of West Africa, but the scarcity of *Pseudacraea eurytus* in the Congo as compared with its relative abundance in Uganda does suggest that its habitat is the lighter forest. If this be so, the lack of continuity of gallery forest across the Congo-Zambesi divide may, as Professor F. E. Zeuner remarked in discussing the subject with me, account for the non-occurrence in " Zambesia." The absence of records from Portuguese East Africa will probably yield to further investigation.

The comparison with *Papilio dardanus* gains interest from the fact that this species does occur in Rhodesia.

A later communication from Mr. Brennan suggested that absence of the correct food-plant from Zambesia may account for the absence of *Pseudacraea eurytus*. *Chrysophyllum* is represented in the basin by *C. bangweolense* near Lake Bangweolo, and *C. argyrophyllum* occurring in dense fringing forest by a perennial stream on a plateau in the central province, and in thickets of *Brachystegia* round Broken Hill. *Mimusops* is common in the fringing forest of the Zambesi and its affluents, but neither it, nor the closely allied *Manilkara* occurring in dry woodland near the Zambesi, are very close to *Chrysophyllum*.

As I have stated previously, the food plant of *Ps. eurytus imitator* in Natal was identified as *Chrysophyllum natalense* Sond. and that in Uganda as a species of *Chrysophyllum* near *kayei* S. Moore.

The larva of *Pseudacraea boisduvali* feeds on *Mimusops* (see Fountaine, 1911).

The distribution of each named form will now be given ; in order to economize space the names of the territories will be known by the letters adopted in the following table. Gambia only occurs once and is written in full. A locality printed in italics signifies that the author has not been able personally to verify the specimen concerned:

Gambia .
French Guinea : F.G. .
Sierra Leone : S.L. .
Liberia : L. .
Ivory Coast : I.C. .
Gold Coast with Ashanti : G.C. .
Togoland : T. .
Dahomey : D. .
Nigeria : Ni. .

Cameroons : C. .
Fernando Po : F.P. .
Spanish Guinea : S.G. .
St. Thomé Isle : S.T. .
Gaboon : G. .
Portuguese Congo : P.C. .
Angola : An. .
French Equatorial Africa : F.E. .
Belgian Congo : B.C. .

Abyssinia : Ab.
South Sudan : S.
Uganda : U.
Kenya : K.
Tanganyika Territory : T.T.
Nyasaland : Ny.
Portuguese East Africa : P.E.
Natal : Na.
Pondoland : P.

Note.—Specimens from the Sese Isles, Lake Victoria, of which accounts have already been given (Carpenter, 1914, 1920*a*) are not included in the totals, except in the case of *grisea*, a new form now separated from *obscura*.

(1) *eurytus* L.

Specimens examined.—M. 46, F. 38. Reported records, 12. Total, 96.

This, the nomino-typical form may be said, generally speaking, to occur throughout West Africa, and is the only form known from Gambia.

Distribution.—Gambia ; F.G., Nzo ; S.L., only the general locality " Sierra Leone " ; L., Monrovia ; I.C., Addah, *Man*, *Toumodi* ; G.C., Accra, Ashanti, Bampata, Coomassie, Huni Valley ; T., " Togoland " ; D., " Dahomey " ; Ni., Ibadan, Isubu, Lagos, Old Calabar, Warri ; C., Ja River (Bitje) ; G., Fernand Vaz (Lake Asebbe), Ogowe, *Tchibanga* ; A., Canhoca ; B.C., Eala, Ituri (30 miles south of Irumu), Kapanga (Lulua), *Landana*, Makala, Manyema (Kongour forest), Nyangwe ; S., Bendere. (The locality " Isubu " on old specimens in the National Collection gave me much trouble, as it is not marked on maps. It seems extremely probable that it refers to the territory of the Sobo tribe in the Niger Delta.)

(2) *ruhama* Hewitson. Examined, M. 49, F. 29. Reported, 19. Total, 97.

G.C., " Gold Coast " ; Ni., Isubu ; C., " South Cameroons," Bitje, Molundu ; S.G., Alen Benito (locality record by Strand, 1914, but the specimen was not typical *ruhama*) ; G., " Gaboon," Brazzaville, Cape Lopez, Etoumbi, Fernand Vaz (Lake Asebbe), Lake Azingo, Lambarene, between Matadi and Stanley Falls, Ngomo, Ogowe, Tchibanga ; An., " Angola," Canhoca ; B.C., Bafwasende, Beni, Ituri, Upper Kasai (Luebo, Nolekesha), Katanga, Kimuenza, Kivu (Kajuduju river), West Kivu, Landana, North-east Lobutu (Lubilinga valley), Ubangi (Duma) ; S., Bendere, Tembura, Yambio ; U., Bwamba valley.

(3) *consanguinea* Aurivillius. Examined, M. 4, F. 12. Total, 16.

Ni., Isubu ; C., " Cameroons " ; G., Lake Azingo ; B.C., Beni, Upper Congo (Bopoto).

This seems an uncommon form.

(4) *striata* Butler. Examined, M. F. 97. Reported, 7. Total, 104.

S.L., " Sierra Leone," watershed of Mabole and Mango rivers 15 miles south of Karrassa ; L., 12 miles east of Monrovia ; I.C., Addah, Bingerville, *Danane* ; G.C., " Gold Coast," Accra, Akropong, Begoro, Gwira, Huni Valley, Kumasi, Kumasi to Kintampo, Obuassi, " Wassaw district," *Winneba* ; T., " Togoland " ; D., Dahomey " ; Ni., Ibadan, Ilesha, Lagos, Ogobahong, Old Calabar, Oni, Oshogbo, Warri ; C., " Cameroons," Bitje, south of Chang, *Duala*, *Molundu* ; G., " Gaboon " ; An., Ambriz, Canhoca ; B.C., *Kimuenza*.

This seems to be very much a " coast " form at present. It is therefore the more interesting that its obvious derivative *youbdonis* (No. 6) occurs in Abyssinia, as evidence of the markedly western affinity of some of the fauna ; it is also interesting that *striata* has not been found in the mountain country of the Sudan-Uganda border, although there is much that is western there. The connection with Abyssinia must be of very much older date, for such western species as occur in South Sudan do not show such a degree of departure from the normal western representatives as in Abyssinia.

(5) *stavelioides* forma nova. Examined F. 1. Total, 1.

More material is required to show whether the distribution of this form agrees with that of its model. The type came from Nigeria, Oni, near Lagos.

(6) *youbdonis* Ungemach. Examined, F. 2. Reported, M. 1. Total, 3.

Ab., *Youbdo*, Gacheb or Gacher river (South-west Abyssinia) ; S., Bendere, Boma Plateau.

In 1935 (p. 363) I alluded to a West African specimen from Isubu as being a male of *youbdonis*. Re-examination shows that it has not all the characters of that form, and it is classed now under *striata*.

(7) *theorini* Aurivillius. Examined, M. 7, F. 12. Reported, 3. Total, 22.

Ni., Isubu, Old Calabar; C., Duala; G., Lake Azingo; S., Bendere.

(8) *epigea* Butler. Examined, F. 8. Reported, 3. Total, 11.

F.G., Konakri; S.L., "Sierra Leone"; G.C., Accra; Ni., Isubu; C., Bitje; B.C., Eala, *Lulua* (Sandoa), Stanley Pool, Uele.

(9) *fulvaria* Butler. Examined, M. 34, F. 23. Reported, 6. Total, 63.

F.G., "French Guinea"; S.L., "Sierra Leone"; I.C., "Ivory Coast," Bingerville, Dimbrok (? = Dimbokro); G.C., Aburi, Accra, Kumasi (Friapere forest), Kumasi to Kintampo; Ni., Isubu; C., "Batouri district" (near Duala), Bitje, Deng-deng, *Lolodorf* (near Duala), Yaunde; S.T., Saint Thomé; G., "Gaboon," Abanga river, Cape Lopez, Fernand Vaz (Lake Asebbe), Lake Azingo, Lambarene, Ogowe river, *Tchibanga*; An., "Angola," Ambriz, Cabinda; F.E., Ubangi; B.C., Beni, *Buta*, Kasai (Luego), Katanga, Lulua-Sankuru; U., Bwamba.

Some of these specimens, from Dimbrok, Kumasi, Bitje, Fernand Vaz, Lambarene and "Angola" might equally well be ascribed to *simulator*, being transitional. Grünberg (1910) recorded one male *fulvaria* from the "Sesse Islands, Lake Victoria," apparently from Ukerewe. It is most unlikely that this was *fulvaria*; it was probably one of the variations that occur so numerously in Sese.

The form *fulvaria* is essentially western, not extending beyond the eastern fringe of the great forest. It is of interest from its occurrence on the island of St. Thomé.

(10) *simulator* Butler. Examined, M. 3, F. 24. Reported, 2. Total, 29.

F.G., near Macenta (Massadou and N'Zébéla); S.L., "Sierra Leone," Mabanta; I.C., "Ivory Coast"; G.C., "Gold Coast," "Ashanti," Accra, Akropong, Huni valley, Kumasi; T. "Togoland"; C., Bitje; G., Fernand Vaz (Lake Asebbe), lower Ogowe (N'gomo); B.C., Ituri forest (Beni), upper Kasai, Katanga, Lokolele, Medje.

This form, like the preceding one, is essentially western. I know of only one record of its occurrence in the eastern part of the Congo, so that it is more western than *fulvaria*, which is more frequently taken in the Ituri forest.

(11) *hobleyi* Neave. Examined, 109. Reported, 18. Total, 127.

B.C., "Ituri," Beni; S., Lotti; U., Ankole (Kalinzu forest), Budama (Busia, Chawoforest), Buganda (Buddu, Entebbe, Kampala, Mabira forest, Sese Isles), Bugishu (Elgon), Bunyoro (Budongo forest), Toro (Bwamba valley, Daro forest near Lake George).

The form *hobleyi* is characteristic of Uganda, but it is occasionally found in the Ituri forest of the Congo, where it meets *fulvaria*.

The above remarks all refer to the male sex, which, until quite recently, was thought to be the only sex for this form. The interesting specimen, kindly lent me for study by Mr. T. H. E. Jackson, captured at Kakamega, Kavirondo, Kenya Colony, led me to search for others among all the female specimens of *poggeoides* that I had seen. But only one female of the *hobleyi* pattern and coloration could be found; it is in the National Collection and was collected at "Ilala, Maramas district, near Mumias," i.e. almost the same spot as the other specimen, which is very interesting. See text-figs. 28A and B.

(12) *hemixantha* forma nova. Examined, 38. Reported, 3. Total, 41.

U., Budama (Chawo forest), Buganda (Buddu, Entebbe, Sese Isles), Buvuma Island, Toro (Daro forest).

Occurs in small proportion with *hobleyi*, but, together with the next form is predominant over *hobleyi* on Buvuma Island.

(13) *opisthoxantha* Carpenter, with transitions to it from *hemixantha*. Examined, 70. Reported, 6. Total, 76.

B.C., Beni; U., Budama (Busia, Chawo forest), Buganda (Entebbe, Mabira forest), Bugishu (Elgon), Buvuma Island, Toro (Daro forest near Lake George, *Ruwenzori*).

A form of occasional occurrence only, except on Buvuma Island, which provided forty-eight of the seventy specimens examined.

(14) *infumata* forma nova. Examined, 7.

U., Entebbe, 4; K., Kavirondo (Mumias), 3. Some specimens of *hobleyi* from the Elgon area approach this form.

(15) *künowoides* Carpenter. Examined, 46.

U., Buganda (Entebbe, "Kyagwe"), Bunyoro (Budongo forest, Munyonyo), Busoga (Jinja).

Apparently confined to Uganda, which is the locality for its model.

(16) *tirikensis* Neave. Examined, 365. Reported, 39. Total, 404.

In the discussion of this form (*antea*, p. 97) it was mentioned that there are two minor forms differing from the type: (A), with less, (B) with greater amount of white on the fore wing. There is also a variety (C) differing by the reddish colour of the basal triangle of the hind wing on the upper side. It seemed worth while to ascertain the distribution of these forms separately, as in the subjoined table. (Var. C may, in other respects, belong to the other forms.) Sese Island

	Type.	*Var. A.*	*Var. B.*	*Var. C.*
Belgian Congo, Beni	2	0	5	3
South Sudan, Bendere	0	0	1	1
South-west Abyssinia, Tirka in Gimira district, and near Meti Chafe	0	0	2	0
Uganda:				
Ankole (Kalinzu forest)	2	0	1	0
Buganda (Buddu)	5	4	3	0
(Entebbe)	77	40	102	1
(Kampala)	1	1	2	1
("Kyagwe")	1	0	0	0
(Sese Isles)	..	..	..	..
Bugishu (foot of Mt. Elgon)	3	0	2	0
Bunyoro (Budongo forest)	18	4	10	1
Busoga (Jinja)	1	1	2	0
Buvuma Island	18	21	7	12
Kigezi (Ruandara forest)	0	0	1	0
Toro (Bwamba valley)	4	0	7	0
(Bugoma forest)	0	1	0	0
(Daro forest near L. George)	6	3	6	0
("Toro")	1	0	0	0
Kenya, Tiriki Hills	3	0	0	0
	142	75	151	19

specimens, owing to their variability, are not included. The specimen of "*togoensis*" figured by Grünberg (1910) seems to be *tirikensis* of the variety C with reddish triangle.

It appears that the form with less white than the type is only half as numerous as either the type or the form with a completed transverse band. It seemed worth while to ascertain the percentage of each form in the west and east, taking the Nile as the dividing line. Thus, the following localities in the preceding table count as eastern (the rest are western)—Jinja, Tiriki, Elgon, Buvuma Island.

		As type.	A, *with less white.*	B, *with more white.*
West of Nile :				
Total	310	117 = 33·7%	53 = 17·0%	140 = 45·2%
East of Nile :				
Total	58	25 = 43·1%	22 = 37·9%	11 = 18·9%
	368	142	75	151

It appears that in the *west* the form with more white on the front wing than in the type predominates over that with less white, whereas the reverse is the case in the *east*. In other words the eastern forms tend to be darker, while the white band is more complete in the west. This is contrary to the usual case of increased darkness in the more humid west.

Now in the east the usual models (*Bematistes macarista* and *alcinoë*) are extremely scarce (cp. the figures for Buvuma Isle, Carpenter, 1947, p. 73) and the only black model sufficiently numerous to be protective is *B. aganice*, which has no white along the inner margin and the white subapical band is very short. Thus it may be that *aganice* has influenced *eurytus* by causing selection of the darker forms.

As regards the variation C in which the basal triangle is markedly reddish on the *upper* surface, it is of occasional occurrence in the west, but remarkably abundant on Buvuma Island in the east; twelve of the forty-five specimens showing it. It exemplifies the close relationship of *tirikensis* to *simulator*. There seems no reason for this except the well known tendency of island faunas to develop differences.

(17) *poggeoides* Poulton. Examined, 60. Reported, 14. Total, 74.

S., Acholi hills, Lotti, Yei; U., Buganda (Buddu, Entebbe, Kampala, *Mabira*, Sese Isles), Bugishu (Mt. Elgon), Bunyoro (Budongo forest), Busia (Chawo forest), Buvuma Isle, Kigezi (Ruandara forest), Toro (*Bwamba valley*, Daro forest near Lake George); K., Kavirondo (Kakamega, *Kitosh*, Mumias, Nzoia river).

This form occurs less frequently in western Uganda than in eastern, and does not seem to occur west of the Semliki. It does not occupy all the area of its model. It is necessary to point out that a specimen in the National Collection labelled "Wad Medani" in the Sudan, collected by Mr. O. W. Snow, certainly did not come from that most unlikely locality. Mr. Snow very kindly supports this statement, and thinks it must have been confused with specimens taken on the mountains along the Sudan-Uganda border, where it is known to exist. This conclusion is supported by a male *Papilio dardanus dardanus* Brown purporting to come from the same locality. Examination of its genitalia, however, showed that it was of the form found in those mountains in South Sudan, and not the form occurring in Abyssinia, either the highlands or the south-west.

(18) *mimo-ras* Ungemach. Recorded, M. 1, F. 1. Total, 2.

Youbdo and Oumbi, Western Abyssinian highlands.

(19) *lachesis* Ungemach. Recorded, F. 2.
Youbdo, Western Abyssinian highlands.

(20) *epaeoïdes* Ungemach. Recorded, F. 1.
Youbdo, Western Absyssinian highlands.

(21) *terra* Neave. Examined, M. 85, F. 106. Recorded, 16. Total, 207.
C., Bitje; G., Ngumie river; B.C., Beni, *Lulua* (*Kafakumba*, *Kapanga*), *Stanleyville*; S., Bendere, Lotti, Yambio; U., Buganda (Buddu, Kyagwe, Mawakota, Sese Isles), Bunyoro (Budongo forest), Toro (Bwamba valley).

This is by far the commonest form in Uganda, which seems to be its headquarters, for although recorded from farther west, it is scarce except in Uganda. Here it is not found east of the Nile, however, nor on Buvuma Island, whence other forms have been obtained.

Besides the above typical specimens, a number of specimens have been examined, transitional to other forms, such as *bicolor*, *tirikensis*, *hobleyi*, or *obscura*. (*Note.*—These do not include the long series from the Sese Isles, separately discussed in Carpenter, 1914, 1920*a*).

Such intermediates number M. 17, F. 34. Total, 51.

They occur in various parts of Uganda as previously listed, and Bendere in Southern Sudan. Also in South-west Abyssinia.

(22) *obscura* Neave. Examined, M. 13, F. 12. Total, 25. Reported (*obscura* plus *grisea*), M.F. 13.

This form, as has been said in the descriptive section, is intermediate between *terra* and the following form *grisea*. Specimens not seen by myself, and classed as " reported " may be either *obscura* or *grisea*. A great many intermediates in various stages between *terra* and *grisea* were reported by myself on the Sese Islands of L. Victoria (Carpenter, 1914 and 1920*a*), and some of them (not now included) correspond with Neave's *obscura*.

U., Buganda (Buddu, Entebbe, Kampala, Sese Isles), Bugishu (foot of Mt. Elgon), Busia, Busoga, Buvuma Island.

(23) *grisea* forma nova. Examined, M. 2, F. 17. Total, 19.

In addition, a large number classed as " *obscura* " in my papers on the Sese Islands of Lake Victoria, together with other specimens not therein included, must now be designated *grisea*; they total, M. 19, F. 45.

U., Buganda (Buddu, Entebbe, Kampala, Mabira, Sese Isles), Bugishu (foot of Mt. Elgon) Buvuma Isle, Toro (Bwamba valley, Daro forest).

A remarkably interesting specimen in the National Collection comes from the western island, San Thomé. The subapical area is almost white, and the pale area of the hind wing is paler than normal, but the specimen can be classed as *grisea*. There is a parallel to this occurrence of a form on west coast islands and the islands of Lake Victoria in the case of *Acraea egina* form *medea* Cramer of Prince's Isle in the Gulf of Guinea and the Sese Island form *alba* Eltringham, (1913, *Trans. ent. Soc. Lond.* **1913**: 412).

(24) *jacksoni* forma nova. Examined, M. 8, F. 9. Reported, M. 2, F. 6. Total, 25.

U., Ankole (Kisale), Bunyoro (Budongo forest), Toro (Bugoma forest).

All specimens seen, except one from Kisale, were taken in Budongo and Bugoma forests.

(25) *bicolor* Aurivillius. Examined, M. 11, F. 19. Reported, 21. Total, 51.

F.P., S.G., Makomo Campo; B.C., Beni, Irumu, upper Lowa valley, Lulua (Kapanga), Uele (Sasa); S., Yei; U., Buganda (Buddu), Bunyoro (Budongo forest), Toro (Bugoma forest, Bwamba valley).

The vast majority of these specimens come from the west of Uganda and the east of the Congo forest, in the neighbourhood of the western rift valley. This is the chief locality for the model, *Bematistes tellus schubotzi* Grünberg. But *bicolor*, being closely related to *terra* from which it is easily derived, may occur sporadically, and a most interesting case is Fernando Po. Here there is an appropriate model in a form of *Bematistes epaea* with white subapical band.

(26) *ruwenzorica* Grünberg. Reported, F. 1.

This remarkable form, from Ruwenzori, is at present represented only by the type specimen.

(27) *victoris* Eltringham. Examined, M. 1, F. 1. Total, 2.

K., Meru, Mount Marsabit.

(28) *rogersi* Trimen. Examined, M. 8, F. 11. Reported, M. 12, F. 13. Total, 44.

K., Gazi, Kwale, Mombasa, Rabai, *Shimba Hills*; T.T., Usambara (Nguelo); Ny., Limbe.

This is an East African form, extending from Mombasa through Usambara into Nyasaland, though records are not continuous between the last two named areas. In Nyasaland it seems to mix with *conradti*, and indeed is not always easy to separate.

(29) *conradti* Oberthür. Examined, M. 11, F. 17. Reported, 9. Total, 37.

T.T., Amani, Lindi, Tanga, Turiani, "Usambara"; Ny., Bandawe, Chinteche, Fort Anderson, Limbe, Mrowi.

This form seems to be confined to East Africa (Tanganyika Territory) and Nyasaland.

(30) *fickei* Weymer. Examined, M. 2. Reported, 1. Total, 3.

T.T., Mhonda, Usigua.

(31) *pondo* forma nova.

The only specimen comes from Cape Colony, Pondoland, Port St. John. Total, 1.

(32) *mlanjensis* Carpenter. Examined, M. 13, F. 12. Total, 25.

Ny., Mt. Mlanje.

(33) *imitator* Trimen. Examined, M. 56, F. (white) 43, (yellowish) 11. Reported, M. 5, F. (white) 5, (yellowish) 3. Total, 123.

B.C., Lodja; P.E., Amatongas, Dondo. It also extends along a tongue of the low country into the Wytchwood Valley, politically just within the Southern Rhodesia border, but faunistically Portuguese East Africa; Na., Durban, Eshowe, Northdene, Pinetown, Zululand; P., Port St. John.

The form *imitator* has always been considered as confined to Natal, and by no means all of that country; however, it extends into Cape Colony, for there are specimens from Port St. John in Pondoland. A specimen in the National

Collection at South Kensington bears data "Belgian Congo, Lodja." If this is the Loja lying to the north of the Sankuru river the record must be looked upon as needing confirmation. I am indebted to Mr. K. M. Penington, Captain R. H. R. Stevenson and Dr. G. van Son for the information that they have never found *imitator* in the Transvaal. But Captain Stevenson has recorded it from Dondo and the Amatongas in Portuguese East Africa, and it extends along a tongue of low country over the boundary into the Wytchwood valley which lies at the foot of the Vumba mountains in Rhodesia not far from Umtali. No other records from Rhodesia are known ; for this I have the authority of Dr. G. Arnold.

There must surely be some links with Nyasaland still to be found, or with Tanganyika Territory via Zululand.

The thirty-three forms of *eurytus* to which names have been given fall into three geographical divisions, western, central and eastern. For brevity's sake the various political territories will be indicated by the letters previously used.

Western area.—Gambia, F.G., S.L., L., I.C., G.C., T., D., Ni., C., F.P., S.G., S.T., G., P.C., An. (part), F.E., B.C. (part).

Only the northern part of Angola, north of Loanda and the Kwanza river, has as yet furnished specimens. Part of the Belgian Congo seems more fittingly classed in the next area, viz. the Ituri forest and the neighbourhood of the great western rift and Ruwenzori mountains.

Central area.—B.C. (part), Ab., S., U., K. (part).

The part of Belgian Congo included here is mentioned above. The part of Kenya Colony is the basin of Lake Victoria.

Eastern area.—K. (part), T.T., Ny., P.E.A., Na., P.

The parts of Kenya here included are Meru and Marsabit, north of Nairobi (but not so far as yet known including Mt. Kenya), and the coastal district. Only the coastal district of Tanganyika Territory from Usambara to Lindi is concerned. The only records from Portuguese East Africa are from the neighbourhood of the Beira-Umtali railway. In Natal and Pondoland only the coastal districts.

Forms of the Western Area.

Eurytus, ruhama, consanguinea, striata, stavelioides, theorini, epigea, fulvaria, simulator, terra, bicolor.

The last two of these belong properly to the central area and are only occasionally found in the western area. A surprising case is *bicolor* from Fernando Po, for it is so very characteristic of the country on each side of the Uganda-Congo border. The form *terra* is so near to *epigea* that its appearance in the western area is not surprising.

Forms of the Central Area.

Eurytus, ruhama, consanguinea, fulvaria and *simulator* all extend into the western section of this area (Ituri forest or Bwamba valley) and the Abyssinian form *youbdonis* obviously derived from *striata*, is another link with the west. South Sudan shows western affinities in the presence of *eurytus* and *ruhama*. Other forms in Abyssinia are *mimo-ras, lachesis, epaeoïdes*.

The characteristic forms of the central area are *hobleyi, hemixantha, opisthoxantha, infumata, künowoides, tirikensis, poggeoides, terra, obscura, grisea, jacksoni, bicolor, ruwenzorica*. It is because several of these occur in the eastern part of the Belgian Congo (the Ituri forest) that that area is considered as one with Uganda, which in its turn contains certain western elements.

Forms of the Eastern Area.

Victoris, *rogersi*, *conradti*, *fickei*, *pondo*, *mlanjensis*, *imitator*.

This area is not linked with the central area, as the latter is with the west, and its forms are peculiar to it. It is unfortunate that so little is known of the forest butterflies between the mountains of Elgon and Kenya, and especially of Kenya itself, where one might expect to find forms linking *victoris* and *rogersi* with the Uganda forms.

Further knowledge of the coastal area of Tanganyika Territory, Portuguese East Africa and Pondoland is much to be desired. Is the form I have here named *pondo* an individual aberration or a well-defined entity? The great variability of *conradti* deserves further study, for it seems an important link.

VIII. THE MIMETIC RELATIONSHIPS OF *Pseudacraea eurytus* AND THEIR BEARING ON THE THEORY OF MIMICRY.

D'Urban (1865) commented upon the absence of mimicry of "*Acraea*" in Africa, but if he had been more familiar with the literature he could hardly have failed to notice the confusion, due to the likeness between *Pseudacraea* and Acraeines, which is revealed in the section on synonymy. Butler, indeed, specially commented upon this in descriptions, but mimicry, in the Darwinian sense, was first expounded by Trimen (1869). On p. 515 he states: "So deceptive is the mimicry of the ♂ *Gea*, by the ♂ *Hirce*, that Godart quotes Drury's figure of the latter as a representation of the *Acraea*. . . . This species of *Panopea* further presents several varieties of the female, which agree with no known examples of *Acraea Gea*, but, strangely enough, are very fair imitators of certain varieties of an allied species, *A. Euryta*, occurring in the localities which they inhabit." In the section on *Acraea Euryta*, p. 516, Trimen continues: "As already mentioned, certain varieties of this abundant *Acraea* (which is known to inhabit Sierra Leone, Ashanti, Old Calabar, the Gaboon and Congo) are the objects of imitation by varieties of *Panopea Hirce*, ♀, received from Congo and Old Calabar. The particular varieties of the *Acraea* that are so imitated are known to inhabit the same localities as the mimickers."

Tylor and Skertchly (1886) figure a female *eurytus* with a species of *Bematistes* (probably *alcinoë*) as model, saying (p. 80) "a normally white butterfly (*Panopaea hirta* [sic]) mimics a normally dark one of quite a different section."

Trimen (1887) discusses *imitator* as a mimic of *Planema aganice*, quoting a remark of Colonel Bowker: "It is quite impossible to distinguish the difference between this butterfly and *Aganice*, either when settled or on the wing; and the first notice you get is the brittle *crunch* between finger and thumb of *Imitator*, or the soft leathery feel of *Aganice*. Death is, moreover, instantaneous with the former, while you may squeeze *Aganice* as long and as hard as you like without effect. . . ." Trimen remarks that *imitator* "is nearly allied to *P. Hirce*, Drury" (see table of synonymy).

Haase (1893, with Plate III, dated 1891) figures *Pseudacraea Hirce* which is " exactly like the corresponding sexes of *Acraea gea*," also figured, and mentions *striata*, *metaplanema* and *fulvaria* with corresponding models.

Aurivillius (1898, p. 531) in a small section on mimicry lists six forms of *eurytus*, as separate species, with their appropriate models.

Trimen (1908) in his description of *rogersi*, which he recognizes as " a near ally of *P. eurytus*, Linn. (*hirce*, Drury)," points out that the differences from *eurytus* " indicate very clearly the mimetic approximation . . . to the common Acraeine, *Planema montana*, Butler, of the same region." He points out that the male *rogersi* is not so good a mimic as the male *eurytus*, but that " it is very noticeable that—as in many other cases of mimicry—the ♀ *rogersi* has proceeded further on the mimetic path, the inner-marginal patch in the fore wings having reached almost as reduced and evanescent a stage as in the ♀ *Pseudacraea imitator*, Trim., in her simulation of *Planema aganice*. The members of the *eurytus*-group of *Pseudacraea* stand out most prominently among mimetic butterflies in the persistency, exactness, and completeness with which they reproduce the pattern and colouring of their models, the very variable and abundant *Planemae*. . . . Every variation in both sexes appears to be faithfully copied throughout tropical and sub-tropical Africa wherever the genus *Planema* prevails . . . it may reasonably be conjectured . . . that the extension of field research will bring to light more mimicries between members of these two genera."

Eltringham (1910) gives an account of each of the *Planema-Pseudacraea* associations known at that time, with coloured plates. Speaking of *striata* he says (p. 71) : " A figure of this *Pseudacraea* appears on Plate III (Diadema) of Hewitson's beautiful series of figures of tropical butterflies, together with the male and female *Pseudacraea eurytus* and the female *Pseudacraea ruhama* [Hewitson, 1868]. All these forms were considered by the author to be varieties of one species, and it was their remarkable resemblance to species of *Planema* which caused him to break through his usual reserve and comment upon their similarity. . . ." The comment is as follows : " May not all the imitators of these scented aristocrats be simply votaries of fashion, aping the dress of their superiors, and, since the females take the lead, ' naturally selecting ' those of the gayest colours." This extraordinary view, as Eltringham points out, shows that Hewitson, like many other critics, did not understand the principle which he criticized, and seems to suggest " a kind of conscious selection on the part of the females for their own adornment. . . ."

Jordan (1911) was the first to state that the numerous forms of *Pseudacraea* which he figured on Plate XXII as thirteen males from West Africa which are considered to belong to at least seven species must be regarded as forms of only one single species, *Pseudacraea eurytus* L. (1758). " The specimens figured do not represent geographical races, although there may be this much geographical in them that only a certain number of the forms occur in the same limited locality. Along with these Pseudacraeas is placed a series of thirteen males of *Planema*, each *Pseudacraea* resembling more or less closely a *Planema* . . . it is startling to find that the *Planema* belong to no less than twelve distinct species." Plate XXIII shows " five white-banded female specimens of *Pseudacraea eurytus* with the females of five species of *Planema*." The next contribution to the subject was by Poulton (1911), and was the first of a series of studies which put the knowledge of *eurytus* as a mimic in Uganda on a numerical basis and led to results giving support to the explanation of mimicry by natural selection. This paper gave an account of a large collection made by C. A. Wiggins and native employees at Entebbe, Uganda, from 23rd May to 31st August, 1909. A slightly amended version of the figures in the 1911 paper is given by Poulton (1912*a*, p. xciii). The specific and varietal names now given are those in the revision of the genus *Planema* by le Doux (1937), who did not accept the new name *Bematistes* propounded by Hemming in Carpenter (1935, p. 435), and for forms of *eurytus* those previously given in this study.

Models.		*Mimics.*	
Group 1.			
B. macarista macarista Sharpe *B. macarista rileyi* le Doux	♂ 81	*hobleyi* *hemixantha* or *opisthoxantha*	32 3
B. poggei nelsoni Dewitz ♂♀	12	*poggeoides*	1
	93		36
Group 2.			
B. macarista ♀	39	*tirikensis*	28
B. alcinoë camerunica Aurivillius ♀	11		
	50		28
Group 3.			
B. tellus eumelis Jordan ♂♀	89	*terra*	18
Group 4.			
B. epaea paragea Grose-Smith	12	*obscura*	0
Totals: *Bematistes*	244	*Pseudacraea*	82
			(= 33·2% of the models)

Dr. Wiggins continued sending great collections to Oxford until May, 1913, and the grand totals are now given. The forms of *eurytus* with yellow hind wing, classed by Poulton with *hobleyi*, are now separated as mimics of the male of *Bematistes aganice ugandae* Van Someren.

Models (*Bematistes*).		*Mimics* (forms of *eurytus*).	
Group 1A.			
m. macarista ♂	197	*hemixantha*	30
m. rileyi ♂	207	*hobleyi*	48
not differentiated ♂	18	*künowoides* with transitions from *hobleyi*	22
macaria hemileuca Jordan ♂	2		
	424		100
Group 1B.			
poggei nelsoni ♂♀	144	*poggeoides*	2
p. poggei ♂	1		
Group 1C.			
aganice ugandae ♂	1	*opisthoxantha* with transitions from *hemixantha*	5

Models (*Bematistes*).		*Mimics* (forms of *eurytus*).	
Group 2.			
macarista (both forms) ♀	270	*tirikensis*	164
alcinoë camerunica ♀	59		
aganice ugandae ♀	6		
	335		
Group 3.			
tellus eumelis ♂♀	670	*terra* ♂♀ with transitions	83
Group 4.			
epaea paragea ♂♀	43	*obscura* ♂♀	3
Grand total	1618		357

Among the Pseudacraeas, which are 18 per cent. of the total butterflies, there are the following specimens transitional between two forms : *hemixantha-opisthoxantha*, 2 ; *hobleyi-künowoides*, 4 ; *terra-obscura* and *terra-hobleyi*, 9 ; total transitionals 15 (= 4·2%).

In 1911–12 I was able to collect on Damba Island, one of the Sese archipelago lying on the equator at the north end of Lake Victoria, only some twenty-five miles south-east of Entebbe. The specimens proved extremely interesting, and were the subject of reports by Poulton (1912*a*, *b*).

I have now re-examined these specimens together with a few more, found when the island collections were finally got together in a special cabinet, after Poulton's account. There are a few adjustments of nomenclature, according to the form names used in the previous pages, and the number of transitional or intermediate specimens has been altered slightly. The forty-three specimens are now shown in two columns, according to whether they correspond with named forms, or are variants. Intermediates between two named forms are given the two names, hyphened.

The *Bematistes* taken during the same period numbered twenty-six.

Specimens from Damba Island, 1912.

NAMED FORMS.		VARIANTS.	
hobleyi	3	*terra-hobleyi*	2
hemixantha	2	*terra-tirikensis*	6
opisthoxantha	1	*terra*, with black bar of f.w. thinned or broken through	2
tirikensis	6	*impleta*	1
poggeoides	1	*terra-grisea* (including Neave's *obscura*)	4
terra	11		
grisea	4		
	28		15

The aberration *impleta* (Grünberg, 1910) is an extreme example of the fusion of the two yellow areas of the fore wing of *terra*, and the presence of a basal triangle indicates that it is a mixture of *terra-tirikensis*. Discussion of these results will be left until data from other islands have been tabulated.

The variants are 34·9 per cent. of the total Pseudacraeas, which equal 62·3 per cent. of the total butterflies of these associations. In 1912–13 I collected on the north-east end of the largest island in the Sese group—Bugalla—the locality known as Lutoboka (Carpenter, 1914). Again I have revised the collections, and the specimens are tabulated as follows

NAMED FORMS.		VARIANTS.	
hobleyi	20	*terra-hobleyi*	54
hemixantha	9	*terra-tirikensis*	61
opisthoxantha	1	*terra*, with black bar of f.w. thinned or broken through	20
tirikensis	35	*terra-grisea* (including Neave's *obscura*)	52
poggeoides	2	*tirikensis-poggeoides*	2
terra	41	*tirikensis-eurytus*	1
grisea	58		
	166		190

The variants form 56·2 per cent. of the total Pseudacraeas, which were 73·4 per cent. of the total butterflies. The specimen mentioned last on the list of variants is a truly remarkable one, for it differs very little from the typical western *e. eurytus*. The white areas of the fore wing are contracted, so that there is a subapical area of the same size as the yellow one of *terra*, and the inner-marginal white area is much like that of *eurytus*, though it does not extend so far forward. The hind wing has a white base, slightly suffused with yellow close to its origin; the black border is much broader than in typical *tirikensis*. The basal triangle on the under side is poorly developed in comparison with *tirikensis*. This specimen alone would show the conspecificity of the West African with the Uganda forms.

During 1914, before the outbreak of war, I was able to collect further examples of these associations on the northern group of the Sese Isles, nearest to Entebbe, viz. the large island of Kome, at its western end, and the smaller islands close to it—Bulago, Ngamba, Kimmi, Tavu (Carpenter, 1920*a*). The collections have been re-examined, and slight numerical adjustments have been found necessary, as greater experience has in some cases ascribed specimens to different categories; the dividing line between a slight variant and a typical specimen is not always easy to fix.

Revised figures are as follows:

NAMED FORMS.		VARIANTS.	
hobleyi	8	*terra-hobleyi*	13
hemixantha	11	*terra-tirikensis*	12
tirikensis	18	*terra*, with black of f.w. thinned or broken through	3
terra	9		
grisea	4	*terra-grisea*	2
	50		30

The variants form 60 per cent. of the total Pseudacraeas, which were 18·3 per cent. of the total butterflies.

It is, perhaps, better to exclude the four small islands, because the number of specimens from each entity is small. Figures for the large Kome alone are :

hobleyi	3	*terra-hobleyi*	13
hemixantha	6	*terra-tirikensis*	12
tirikensis	9	*terra*, with black of f.w. thinned or broken through	3
terra	9		
grisea	2	*terra-grisea*	2
	29		30

The variants on Kome Isle alone form 50·8 per cent. of the Pseudacraeas, which were 22·9 per cent. of the total butterflies.

The war put a stop to work on the islands, but during 1915 I was in camp on the west coast of Lake Victoria, in Buddu, where the Malabigambo or Tero forest offered good collecting. The specimens have been re-examined save that as the whole of the *Bematistes* could not be found I have restated the original figure given (Carpenter, 1920*a*). Out of the 13 Pseudacraeas, 1 was *hobleyi*, 8 *terra*, 3 *terra* with very slight thinning away of the black on the fore wing, and 1 was *terra-hobleyi*. All the variants were very close to normal *terra* ; they form 30·8 per cent. of the Pseudacraeas, which constitute 12·7 per cent. of the total butterflies. But the numbers are small and probably inadequate for comparison.

After the war I was able to revisit the Kome group in 1918–19, and to obtain the following specimens ; again they are set forth as a result of revision, and the figures differ slightly from those previously cited ; only Kome Island (its western end) is given, as very few specimens were obtained from smaller islands :

Named Forms.		Variants.	
hobleyi	6	*terra-hobleyi*	11
hemixantha	3	*terra-tirikensis*	10
tirikensis	4	*terra* with black bar on f.w. thinned or broken	4
poggeoides	1		
terra	9	*terra-grisea*	3
grisea	2	*tirikensis-poggeoides*	1
	25		29

The variants are 53·7 per cent. of the Pseudacraeas, which form 68·5 per cent. of the total butterflies.

Lastly, a collection from Buvuma Island, much to the east of all the islands hitherto considered, was obtained in 1946, as follows :

Named Forms.		Variants.	
hobleyi	0		
hemixantha	13	*hemixantha* to *opisthoxantha*	30
opisthoxantha	16		
tirikensis	43		
poggeoides	2		
grisea	3		
	77		30

These figures are increased by 1 *tirikensis* and 1 *hemixantha-opisthoxantha* (and also one *B. poggei* ♂) over the figures in Carpenter (1947) as these had escaped being set and were found later. The variants are 28·0 per cent. of the Pseudacraeas, which are 42·7 per cent. of the total butterflies.

Putting the results together we get the following table :

Locality.	*Pseudacraea percentage in the association.*	*Variant Pseudacraeas percentage of total Pseudacraeas.*
Entebbe (on mainland)	18·0	4·0
Damba Island	62·3	34·9
Bugalla Island	73·4	56·2
Kome Island, 1914	22·9	50·8
,, ,, 1918–19	68·5	53·7
Buvuma Island, 1946	42·7	28·0

It is at once apparent that there is an inverse ratio between the numbers of Pseudacraeas in the mimetic association and the numbers of them which depart from strict likeness to the models.

There is a slight difference in detail from the previous account given in 1920. Firstly, as I have said, a revision of the Pseudacraeas resulted in a greater number being classed as variants owing to smaller differences now being better appreciated. This has nullified the statement (*loc. cit.*, p. 94) about the "difference between the proportions of models and mimics on Kome Island in 1914 and 1918–19."

Secondly, in the present account I have not included the few specimens from the four small islands around Kome, for the reason already given.

With this exception the island localities agree in showing greater variability of *Pseudacraea* with the comparative scarcity of *Bematistes*. When this first became clear, from the Damba specimens, Poulton wrote (1912*a*, p. 94) that, inasmuch as the Damba specimens were collected in almost the same months as the series from Entebbe with which he compared them, "it is highly improbable that these remarkable differences are connected with climate or season of the year . . . The most probable explanation appears to be that, in the condition of the jungle on Damba Island, there is something unfavourable to Planemas [*Bematistes*], and that, *in the absence or relative scarcity of the models, the mimetic resemblance of the Pseudacraeas is no longer rigidly maintained by selection*. [Italics by G. D. H. C.] The pattern of *Ps. terra* is found among the protean mimetic forms of *eurytus*, L., on the west coast. . . . I suggest that in an area where these mimetic patterns are less strongly selected, there is a tendency, checked elsewhere, for them to run into each other, and also to move in the direction of the western *eurytus* forms, from which there can be little doubt that the mimetic Pseudacraeas of Uganda originally developed." The opinion voiced in the last few words was strikingly confirmed by the variant female taken on Bugalla Island (*vide supra*).

This important conclusion was discussed later (Manders, 1915). It has received support from a study of the very variable subspecies *polytrophus* Rothschild and Jordan of *Papilio dardanus* Brown (Ford, 1936), in which it is stated "there is a deficiency of models relative to mimics in subspecies *polytrophus* as compared with a race in which the mimicry is more fully developed."

Precise Relationship Between Species of Bematistes *and the Appropriate Forms of* Pseudacraea eurytus.

The earlier writers in some cases commented upon the similarity of Pseudacraeas to species of *Bematistes* in the same area. Coincident distribution is, of course, necessary for mimicry, provided that it is not insisted that the coincidence shall be complete to the last detail. A certain amount of latitude must be allowed, e.g. in the case of *Papilio dardanus trophonissa* Aurivillius, which occurs in thicker cover than that usually frequented by *Danaus chrysippus* L. But no numerical comparison was made until the great collections of C. A. Wiggins at Entebbe were examined.

These have been tabulated above (p. 118), and it will be useful to state the type of coloration for each grouping.

Group 1A, B, have an orange or orange yellow band crossing the front wing and a white bar across the hind wing. In 1A the tint of the band on the fore wing is richer and the direction more antero-posterior than in 1B. In 1C the hind wing is also orange. Group 2, consisting of females only, is black and white. Group 3 is orange, but the pattern of the fore wing consists of an oblique subapical bar and an inner-marginal patch, and the hind wing has no basal triangle. Group 4 has somewhat the same pattern, but the pale areas are contracted and dull yellow or yellowish white, and there is a small basal triangle on the underside of the hind wing.

In the first place it may be said that, taking regional distribution, there is close correspondence. Group 1 is characteristic of Uganda, and the adjoining part of the Belgian Congo and rare in West Africa. Group 2 is widely distributed, although the species are different in some cases in the two regions. Group 3 depending on *Bematistes tellus* has its headquarters in Uganda, and examples in West Africa are scarce. Group 4 is peculiar to Uganda and the Congo border. On the other hand, the characteristically West African *Bematistes e. epaea*, with its mimic the nomino-typical *eurytus*, does not occur in Uganda, nor the form *striata* mimicking *Bematistes vestalis*. But, unfortunately, there are no West African collections from which statistical evidence can be obtained to show, as the following data will show (Table II), the correspondence in any one locality between numbers of models and their appropriate mimics.

The table shows the following correspondences between the prevalence of species of *Bematistes* and forms of *Pseudacraea eurytus*. At Entebbe the combinations 1A + 1B, with the females of 1A as 2, are responsible for the majority of models and mimics, while 3 follows fairly closely, and 1C and 4 are negligible. See Poulton, 1926, p 23 for increase of *aganice* at Entebbe.

On Bugalla Island the chief place is taken by 4, with 3 next, and the rest on a lower level, 1C again being negligible.

On Buvuma Island there is a great increase in 1C (*aganice*), of which the black and white female helps to swell 2, which in *Pseudacraea* is particularly well represented. A point of interest is that 1B is so unusually large that it is

TABLE II.

	Group.	*Bematistes.*			*Pseudacraea.*			Remarks on the *Pseudacraeas.*
		Total.	Number belonging to group.	Percentage of total.	Total.	Number belonging to group.	Percentage of total.	
Entebbe.	1A, 1B	1618	569	35·2	357	102	28·6	The variation is so slight in the 15 variants that the groups are not affected.
	1C	,,	1	—	,,	5	1·4	
	2	,,	335	20·7	,,	164	45·9	
	3	,,	670	41·4	,,	83	24·4	
	4	,,	43	2·6	,,	3	0·8	
Bugulla Island.	1A, 1B	129	12	9·3	166	31	18.7	Some of the variants are not reconcilable with any group. But if those varying only slightly were attached to groups the numbers in Groups 3 and 4 would be much increased and 1 and 2 proportionately diminished.
	1C	,,	0	0	,,	1	0·6	
	2	,,	9	6·9	,,	35	21·1	
	3	,,	33	25·6	,,	41	24·7	
	4	,,	75	58·1	,,	58	34·9	
Buvuma Island.	1A	144	3	2·1	77	13	16·9	In Group 1A the forms with white band on h.w. not touched with yellow have been swamped by the forms with partly or entirely yellow h.w. composing 1B and 1C. 30 specimens have more yellow than *hemixantha*, but not quite so much as *opisthoxantha*.
	1B	,,	21	14·6	,,	2	2·6	
	1C	,,	70	48·6	,,	16	20·8	
	2	,,	45	31·2	,,	43	56·0	
	3	,,	1	—	,,	0	0	
	4	,,	4	3·5	,,	3	3·9	

N.B.—There are two more Pseudacraeas and one more *Bematistes* than are shown in Carpenter (1947). They had eluded the setting board and were found in papers later.

shown separately for the first time. The chief point about the Buvuma specimens lies in the Pseudacraeas of Group 1C. Although these are shown as only 16 per cent. because of strict accuracy in not including variants, the influence of the male *aganice* is greatly emphasized by the fact that among the males which constitute 1A *not one* has the pure white bar on the hind wing (as in *m. macarista* and *hobleyi*). Moreover, in addition to the half-yellow *hemixantha*, of which 13 are listed, there are 30 specimens with still more yellow which are not shown because they are variants on the way to *opisthoxantha*.

Regarding the greater number of *B. poggei* and *eurytus poggeoides* on Buvuma Island, it is interesting to refer to a small collection from the Eastern Province of Uganda in which I developed (Carpenter, 1924) a point to which Neave (1912) had drawn attention, namely, that in the absence of a black and white model the female form *tirikensis* tended to be replaced by *poggeoides* in accordance with the greater abundance of *B. poggei*.

In other parts of Uganda large collections have been obtained, but as it is not certain that they were made strictly without selection, statistical evidence is lacking. But many points of interest arise, showing certain similarities between *Bematistes* and *Pseudacraea*.

Thus in the Budongo forest (Carpenter, 1936) east of Lake Albert, which must be a portion of the great western forest, as it contains chimpanzees and pottos, there is a form of *B. epaea* intermediate between the western *e. epaea* and the Uganda *e. paragea*. Male and female alike have the paler areas reduced in size and cream coloured (Carpenter, 1935*b*). This is faithfully copied by the form of *eurytus*, which I have named *jacksoni*. Both occur in another western forest (Bugoma), but *jacksoni* is not found apart from its model.

A very striking *Bematistes*, *tellus schubotzi* Grünberg, occurs in the Budongo forest and along the valley country south of Lake Albert. It differs from *t. tellus* chiefly by the brilliantly shining white subapical area on the fore wing of the female. Associated with it is the corresponding form *bicolor* of the *Psendacraea*.. Forms approaching *bicolor* may be found very occasionally as rare variants in other parts of Uganda, but it is not fully established except in the presence of *B. schubotzi*. Therefore it is particularly interesting to find that there are specimens of *bicolor* and a form of *epaea* with the same coloration (*insularis* Aurivillius) in the National Collection from Fernando Po !

Again referring to the Budongo forest, all the specimens of *B. macarista* that I have seen (11) are of the form *m. macarista* with white hind wing bar, and so are the appropriate forms of the mimic (*hobleyi*, 5). Along the mountains of the Sudan-Uganda border *B. epaea* occurs in some rather interesting varieties, and corresponding variations in *Pseudacraea eurytus* also occur there.

In Abyssinia Ungemach figured in colours (1932) a striking pair of model and mimic which are not known outside that locality.

The restriction of the *Pseudacraea* in Natal to a single sexually dimorphic form agrees with the fact that in that country there is only the one species of *Bematistes*, sexually dimorphic. What a contrast to the wealth of forms in West Africa !

There is not enough knowledge of details of distribution in the west for any statements to be made comparable with the preceding, but it is clear that both *B. vestalis* and its mimic *striata* are truly " coast " species and do not range very far into the Congo.

On the other hand, certain very striking species of *Bematistes* lack the appropriate mimetic form of *Pseudacraea*, and chief among these is *B. quadricolor* Rogenhofer. This is abundant in the mountain country of western Uganda and the adjoining parts of the Congo, and again on the highlands of East Africa. It has apparently influenced *Acraea johnstoni* Godman to produce the form *butleri* Aurivillius, which is only found with *quadricolor*. Now, with one exception, no form of *eurytus* is known which corresponds to *quadricolor*. Although *eurytus* does not fly at the higher levels frequented by *quadricolor* their ranges do overlap on the east side of Lake Victoria, and in Usambara. The exception is extremely interesting. Grünberg (1912) figured, under the name *ruwenzorica* a specimen from the west side of Ruwenzori at 1800 metres, which most clearly mimics *quadricolor*. But no other specimen has yet come to light, and accessions are much wanted. Dr. van Someren is of the opinion that the form *victoris* is a mimic of the race of *quadricolor* occurring in the same locality, *leptis* Jordan, but more observations are required.

Another *Bematistes* for which no mimic is known is *B. formosa* Butler, a large species with a brown band across the fore wing and a very sharply defined, narrow, pure white band on the hind wing. Though a large species, it does not appear to be abundant, which may explain the absence of a mimetic *Pseudacraea* ; the type of coloration would seem to be well within the scope of the variations in *Ps. eurytus*.

The coincidence between the coloration of *Bematistes* and *Pseudacraea* in the same area induces opponents of the Darwinian explanation of mimicry to put forward the alternative explanation that the agreement is due to exposure of the two types of butterfly to similar environment. This facile and commonly used argument does not bear investigation. The appearance of a butterfly does not result from the environment in which the imago lives; the pattern is laid down in the only actively growing stage, the larva. It is not at all certain that the environmental influences are the same for a *Bematistes* as for a *Pseudacraea*. I found larvae of *B. poggei* on Damba Island feeding on a low-growing creeper, while *eurytus* larvae feed on a forest tree at a very different level. The absurdity of this argument will be obvious if it is applied to Lycid beetles and their mimics, which between them exemplify almost every possible variety of larval food and environment and yet have similar coloration in the adult.

The remarkable variation, and departure from strict likeness to the model, in an area where the latter are scarce, militates against a purely environmental explanation. The changes in proportions of the different species of model and forms of mimic in localities so near as Entebbe and Bugalla Isle do not support an environmental explanation of mimicry. For instance, the Group 4 is very scarce at Entebbe, but abundant on Bugalla Isle and scarce again on Buvuma. But on Buvuma the male form with orange hind wing (*opisthoxantha* and transitions to it) is vastly predominant, while very very scarce elsewhere. This is associated with a species not of any account as model at Entebbe, and absent from Bugalla.

The theory might be called upon to explain presence or absence, but its application to relative differences in numbers and variability seems difficult.

Consideration of the forms on Buvuma Island is appropriate. The common male form *hobleyi* of the *Pseudacraea* has the hind wing bar pure white, or slightly yellow anteriorly in the form *hemixantha*. Such specimens are widely spread over the mainland of Uganda, especially west of the Nile, and, on the theory, owe their whiteness to that country. On Buvuma Island, further eastward, the male never has pure white hind wings, but ranges from *hemixantha* to *opisthoxantha*, in which the hind wing is wholly yellow; this would be ascribed to the action of Buvuma conditions. The female *Pseudacraea* common in western Uganda, the black and white form *tirikensis*, is also presumably a product of Uganda west of the Nile. On Buvuma Isle it still remains abundant, i.e. whereas according to theory Buvuma conditions have altered the male, the female has not responded.

An explanation is to be found for both sexes in the superabundance of an eastern species of *Bematistes* (*aganice*), of which the male provides a new model for the *Pseudacraea* while the latter has a model for its female so little different from the usual model that no change has been effected in that sex. If, however, a purely environmental explanation is sought, it has to admit that the male but not the female has responded on Buvuma Island. Consideration of other species shows how the environmental explanation fails to meet facts. The dull Uganda race *paragea* of the widespread *Bematistes epaea* appears to be a weak protector for *eurytus* in most parts of Uganda, compared with other *Bematistes*. Jordan (1911) pointed out that *Elymniopsis phegea* F. has a form in West Africa resembling *Bematistes e. epaea*. But in Uganda *phegea* does not mimic the local race *paragea* of *epaea*, but follows more abundant models.

The form *bicolor* of *Pseudacraea eurytus* is also significant. It does appear occasionally as a rare variant of *terra*, but in the absence of a model it remains a rarity. But in two such distinct areas as the great western rift and the island of Fernando Po, in the presence of a similar species of *Bematistes* it takes its place as a mimic.

Another explanation of mimicry that seems at first sight plausible is that it is merely an expression of parallel variation between species not very far removed in relationship. This is not the place to counter that argument from examples outside the scope of the present study. But a remark by Trimen is so appropriate that allusion to it may be made here. He points out (1897, **1** : 38) that the *males* of *Papilio echerioides* Trimen and *P. cynorta* Fabricius are very much alike, but the *female* of the former mimics *Amauris*, of the latter, *Bematistes*. It may be pointed out that, while it is true that all forms of *eurytus* correspond to species of *Bematistes*, this is not the case if the genus *Pseudacraea* as a whole be considered. Reference to the table, p. 73, in the earlier part of this study shows that species of *Pseudacraea* mimic species of two genera of ACRAEIDAE and two of DANAINAE.

There is also illustrated by *Pseudacraea eurytus* the phenomenon of secondary mimicry. This may be looked for in an association containing numerous distinct species with a general uniformity of appearance resembling some predominant model. The smaller details of coloration and pattern, however, may not be precisely similar, and sometimes it is found that one of the mimics of the primary model has certain minor peculiarities which are also borne by another member of the group, or even by a variety of another member, that member also appearing in the group without those slight differences.

I have previously pointed out (1947, pp. 64–5) that large mimetic associations should be regarded as a chain rather than a " ring," and that secondary mimicry supports this view. Among the Uganda mimics of *Bematistes macarista* and *poggei* there is a large, robust, species of *Pseudacraea*, the form *künowi* Dewitz of the western *gottbergi* Dewitz. The orange band of the forewing of this species is sharply angled and narrowed anteriorly. Also in Uganda there occurs, with *künowi*, a form of *eurytus* in which the orange band of the fore wing, instead of being gently curved and of approximately the same width anteriorly as posteriorly (as in *hobleyi*), is sharply angled, and narrowed anteriorly as in *künowi*, and it has therefore been named *künowoides* (Pl. II, fig. 16). The robust bodily structure of *künowi*, its larger size and vigorous habit, suggest that it may have served as a model (for minor features) for a form of *eurytus*, while both are still mimics of the relatively more distasteful *Bematistes*.

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ADDENDUM.

Goeze (*loc. cit.*) lists two references which I have been unable to consult in the original. They are :

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Cathol. E. p. 322, *Euryta.*

Mr. A. C. Townsend of the General Library, British Museum (Nat. Hist.) (*in litt.*, 1.iv.1947), has very kindly identified these works as "Onomatologia medica completa, seu Onomatologia Historiae Naturalis, oder vollständiges Lexicon, des alle Benennung der Kunstwörter der Naturgeschichte . . . erkläret," etc., 7 bde. Ulm, etc. 1758–77. 8° ; and "Catholicon, ou dictionnaire universal de la Langue Françoise—oder Französisch—Deutsches Universal-Wörterbuch der Französischen Sprache," 9 tom. Hamburg, 1771–2. [By J. J. Schmidlin.] 4°.

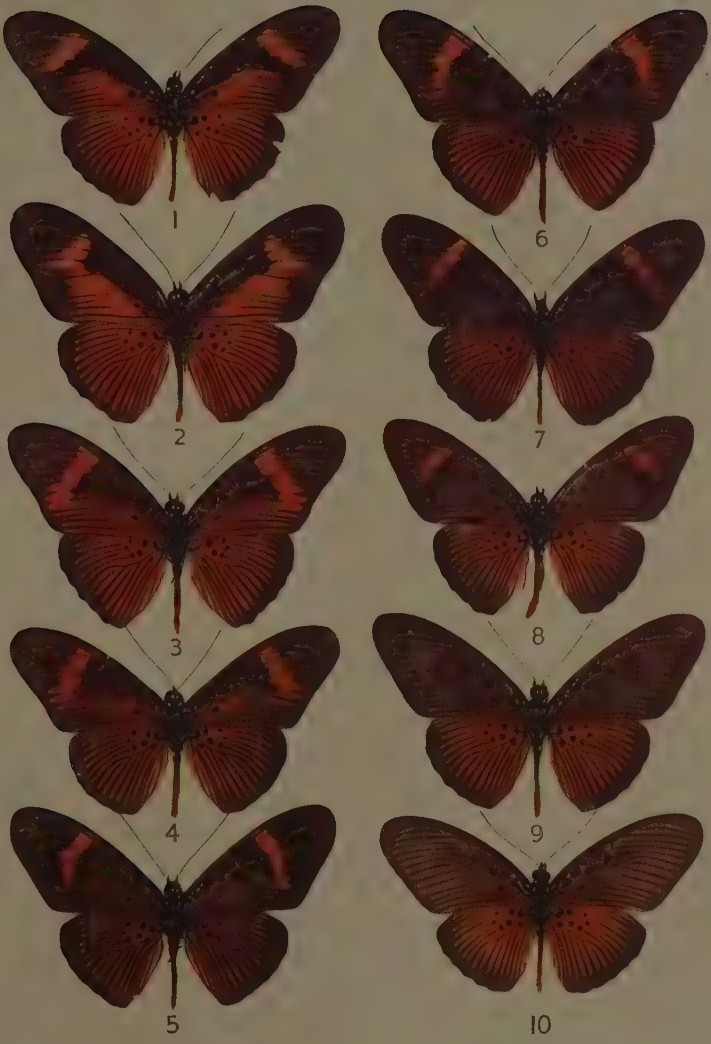
Neither are in the library of the Natural History Museum, but Mr. Townsend states that both are in the British Museum (Bloomsbury), the former at pressmark 723, h. 1–3, and the latter at 69, c. 8, though it is presumably incomplete as only vols. 1–7 [A–H] are noted under Schmidlin in the catalogue.

PLATE I.

Male forms of *Pseudacraea eurytus* (L.) West Africa.

FIG.

1. *eurytus* L., West Africa. Purchased. (O.U.M.)
2. Transitional from *eurytus* to *ruhama*, Cameroons, Bitje, Ja River, 2000 ft., dry season, January–March, 1907, G. L. Bates. (B.M.)
3. *ruhama* Hew., atypical. French Congo, Lambarene, Harrington. (B.M.)
4. *ruhama* Hew., atypical. Gaboon, Cape Lopez. (B.M.)
5. *ruhama* Hew., typical. Data as for 2. (B.M.)
6. *ruhama* Hew., atypical. Gaboon, Lake Azingo, December, 1907, Dr. Ansorge. (B.M.)
7. Transitional from *ruhama* to *theorini*. Belgian Congo, Kasai, Nolekesha, 27th March, 1919, Scheut Mission. (B.M.)
8. *theorini* Auriv., Cameroons. (B.M.)
9. Transitional from *theorini* to *striata*. Cameroons. (B.M., Crowley bequest.)
10. *striata* Btlr. Nigeria, near Lagos, dry season, 17th February, 1911, W. A. Lamborn. (O.U.M.)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Male forms of *Pseudacraea eurytus* (L.). West Africa.

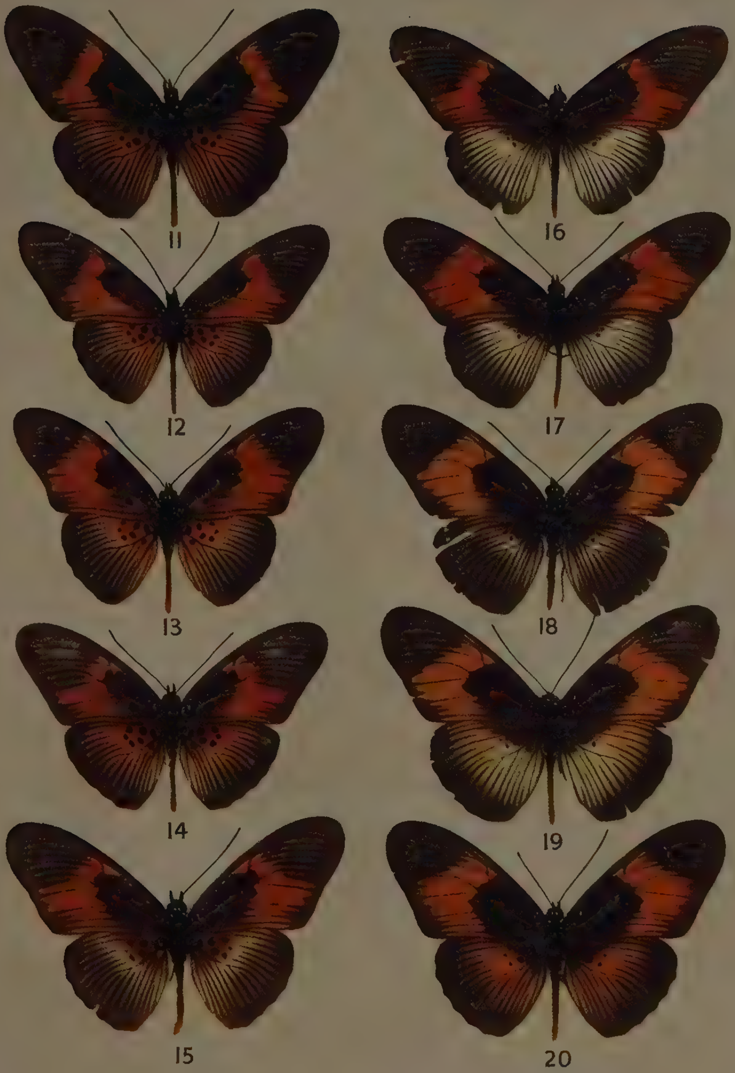
(About ⅝ natural size).

PLATE II.

Male forms of *Pseudacraea eurytus* (L.). West and East Africa.

FIG.

11. Transitional from *ruhama* to *fulvaria*. French Cameroons, Bitje, 3° N., 12° E., wet season, 1926, G. L. Bates. (B.M., Joicey bequest.)
12. *fulvaria* Btlr., typical. Belgian Congo, Haut-Kasai, Lulua, Sankuru, 1902–4, Landbeck. (B. M., ex Oberthür.)
13. Transitional from *fulvaria* to *simulator*, French Congo, Lambarene, Harrington. (B.M.)
14. Transitional from *fulvaria* to *simulator*, Gold Coast, Ashanti, Coomassie to Kintampo, April, 1899, Northcott. (B.M.)
15. *simulator* Btlr. Angola. (B. M., ex Hewitson.)
16. *künowoides* Crpntr. Uganda, Bunyoro, Budongo forest, October–November, 1939, native collector for T. H. E. Jackson. (O.U.M.)
17. *hobleyi* Neave, typical. Uganda, Entebbe, 7th August, 1909, native collector for C. A. Wiggins. (O.U.M.)
18. *infumata* forma nova. Type. Uganda, near Kampala, September, 1934, T. H. E. Jackson. (O.U.M.)
19. *hemixantha* forma nova. Type. Uganda, Buvuma Island, Magyo, 15th February, 1945. Native collector for G. D. Hale Carpenter. (O.U.M.)
20. *opisthoxantha* Crpntr. 3rd February, 1945. Locality etc., as for 19. (O.U.M.)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Male forms of *Pseudacraea eurytus* (L.). West and East Africa.

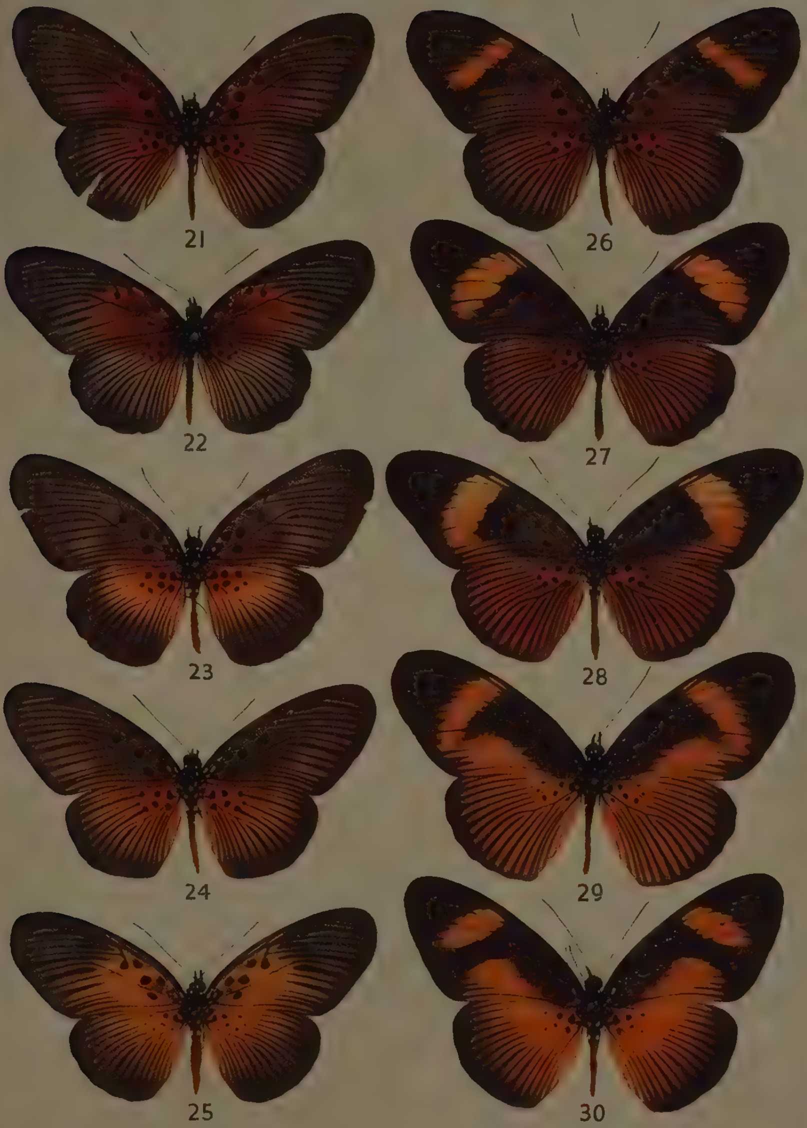
(About $\frac{5}{8}$ natural size).

PLATE III.

Female forms of *Pseudacraea eurytus* (L). West Africa and Abyssinia.

FIG.

21. *striata* Btlr., typical. Liberia, 12 miles east of Monrovia, July, 1926. W. Portal Hyatt. (B.M.)
22. *youbdonis* Ung., South-west Abyssinia, near Gacher (Gacheb) river, 7° 1′ N., 35° 22′ E., 3800 ft., 15th February, 1927, A. Hodson. (O.U.M.)
23. *striata* Btlr., atypical. Cape Coast. (B.M.)
24. *striata* Btlr., atypical. Nigeria, Oni, near Lagos, dry season, 31st December, 1910, W. A. Lamborn. (O.U.M.)
25. *stavelioides*, forma nova. Type. Nigeria, Oni, near Lagos, 8th March, 1911, W. A. Lamborn. (O.U.M.)
26. *consanguinea* Auriv. Isubu. (B.M., ex Distant.)
27. *ruhama* Hew., atypical. South-west Sudan, Tembura, 10th December, 1918. (B.M., ex Oberthür.)
28. *ruhama* Hew., typical. Gaboon, Ogowe, 1890, L. Gazengel. (B.M.)
29. Transitional from *ruhama* to *epigea*. Cameroons, Bitje, Ja River, 2000 ft., G. L. Bates. (B.M., ex Bethune Baker.)
30. *epigea* Btlr., typical. French Guinea, Konakri. (B.M., Joicey bequest.)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Female forms of *Pseudacraea eurytus* (L). West Africa and Abyssinia.

(About ⅝ natural size).

PLATE IV.

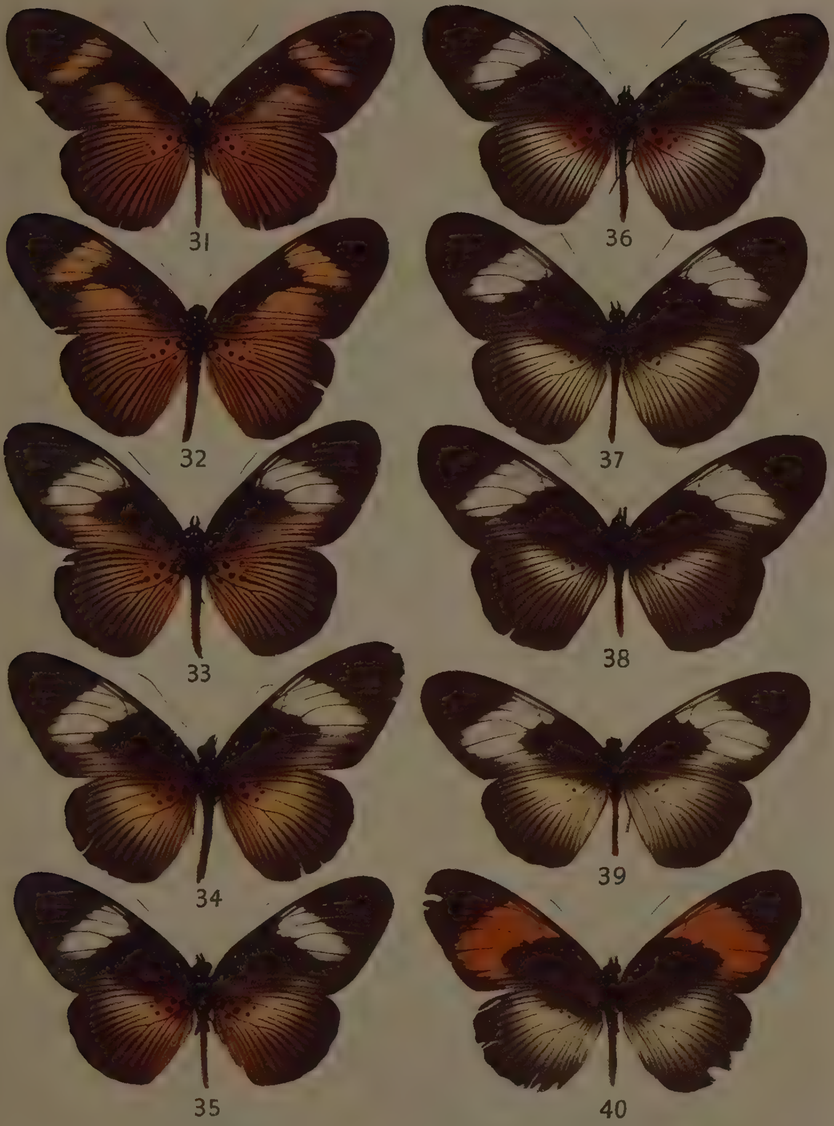
Female forms of *Pseudacraea eurytus* (L.). West Africa, Uganda, South Sudan.

FIG.

31. *epigea* Btlr., pale, atypical. Tanganyika, Région de M'Pala. (B.M., ex Oberthür.)
32. Transitional from *epigea* to *fulvaria*. Belgian Congo, Stanley Pool to Lukolela, 1894, Harrison. (B.M.)
33. *fulvaria* Btlr., typical. French Congo, Lambarene, Harrington. (B.M.)
34. Transitional from *fulvaria* to *simulator*. Sao Thomé Island, 28th September, 1932, W. H. T. Tams. (B.M.)
35. *simulator* Btlr., typical. Belgian Congo, Haut Congo, Basankusu, Bongandanga, 22nd February, 1933, Gertrude Vinall. (O.U.M.)
36. *simulator* Btlr., atypical. Belgian Congo, Katanga, January, 1929. (B.M., Joicey bequest.)
37. *tirikensis* Neave, atypical, Uganda, Buvuma Island, Magyo, 30th January, 1945, native collector for G. D. Hale Carpenter. (O.U.M.)
38. *tirikensis* Neave, typical. Uganda, Entebbe, 27th September, 1910, C. A. Wiggins. (O.U.M.)
39. *tirikensis* Neave, atypical. As 38, except date 8th August.
40. *poggeoides* Poulton, South Sudan, Mongalla Province, Acholi Hills, Lotti, 3000 ft., July, 1930, I. G. Owen. (O.U.M.)

Note.—Figs. 36–39 show a yellowish border to the white on the hind wing which is not apparent in the butterflies. It seems possible that, as Figs. 37–39 are the Uganda representatives of the Congo forms Figs. 35–36 in which, to the eye, the yellow has become white, the chemical change is incomplete and still reveals some yellow in the process of colour reproduction.

Plate IV.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Female forms of *Pseudacraea eurytus* (L.). West Africa, Uganda, South Sudan.

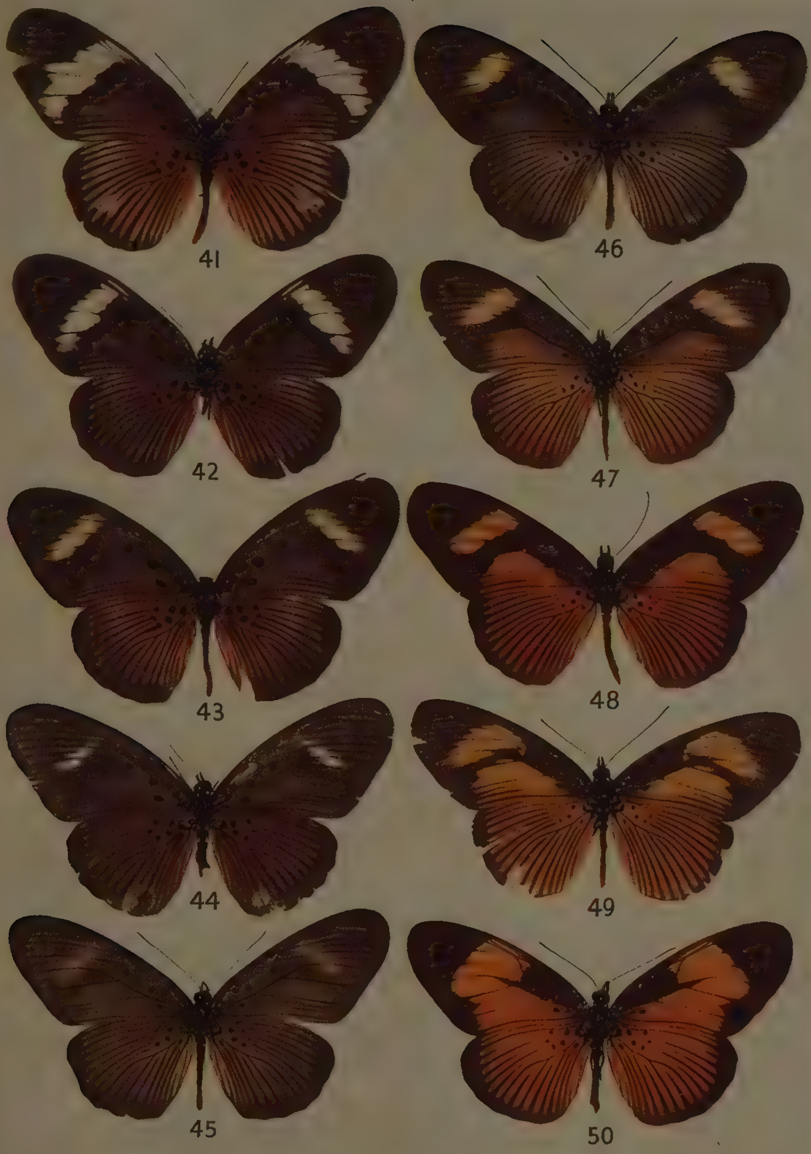
(About $\frac{5}{8}$ natural size).

PLATE V.

Female forms of *Pseudacraea eurytus* (L.). West and East Africa.

FIG.

41. *consanguinea* Auriv., atypical. Gaboon, Lake Azingo, December, 1907, Dr. Ansorge. (B.M.)
42. Transitional from *consanguinea* to *theorini*. Data as 41.
43. *theorini* Auriv. Cameroons. (B.M.)
44. *theorini* Auriv. Isubu. (B.M., ex Distant.)
45. *obscura* Neave, atypical. Uganda, "Port Alice" [Entebbe], 19th July, 1894, Dr. Ansorge. (B.M.)
46. *grisea* forma nova. Type. Uganda, Sese Isles, Bugalla, Lutoboka, 12th March, 1912, G. D. Hale Carpenter. (O.U.M.)
47. *obscura* Neave, typical. Data as 46, except date 10th August. (O.U.M.)
48. *terra* Neave, typical. Uganda, Entebbe, 18th August, 1911. C. C. Gowdey. (B.M.)
49. *terra* Neave, atypical. Data as 46, except date 13th November. (O.U.M.)
50. ab. *impleta* Grünb. Uganda, Sese Isles, Kome Island, August, 1926, Mr. and Mrs. W. C. Simmons. (O.U.M.)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Female forms of *Pseudacraea eurytus* (L.). West and East Africa.

(About ⅝ natural size).

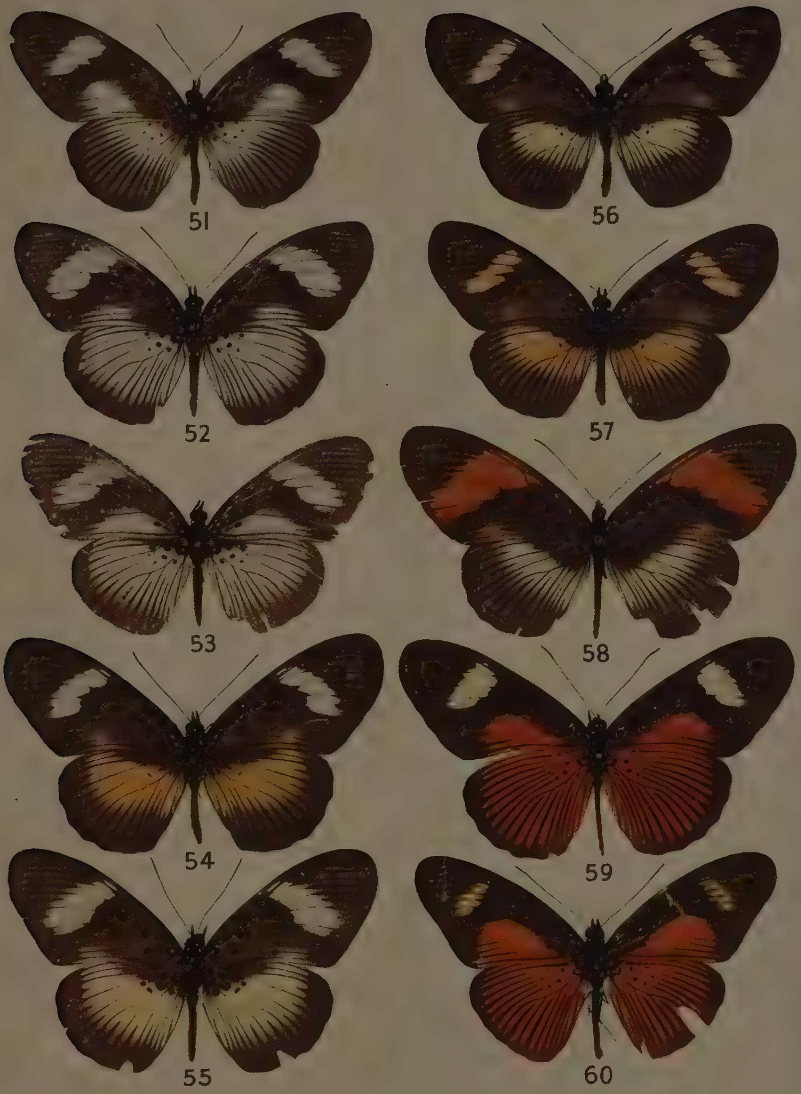
PLATE VI.

Forms of *Pseudacraea eurytus* (L.).

FIG.

51. *eurytus* L., ♀, typical. Sierra Leone Protectorate, 1910–13, Charles A. Foster. (O.U.M.)
52. *rogersi* Trim., ♀, typical. Kenya Colony, south of Mombasa, Kwale, March, 1939, T. H. E. Jackson. (Coll. Jackson.)
53. *rogersi* Trim., ♀, atypical. As 52.
54. *conradti* Oberth., ♀. Tanganyika Territory, Morogoro district, Turiani, 9th June, 1933, B. D. Burtt. (O.U.M.)
55. *mlanjensis* Crpntr., ♀, typical. Nyasaland, Mlanje, 27th January, 1913, S. A. Neave. (B.M.)
56. *imitator* Trim., ♀, typical. Natal, Durban, bred 20th April, 1910, A. D. Millar. (O.U.M.)
57. *imitator* Trim., ♀, atypical. Data as 56 except date 6th February. (O.U.M.)
58. *poggeoides* Poult., ♀, atypical. Uganda, Buddu, Malabigambo forest, Katera, November, 1935, T. H. E. Jackson. (O.U.M.)
59. *bicolor* Auriv., ♀, Belgian Congo, Ituri forest, Beni, October, 1946, T. H. E. Jackson. (O.U.M.)
60. *bicolor* Auriv., ♂. Fernando Po, Timbabé, near Santa Isabel, 20th July, 1916, G. H. Bullock. (O.U.M.)

Plate VI.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Forms of *Pseudacraea eurytus* (L.).

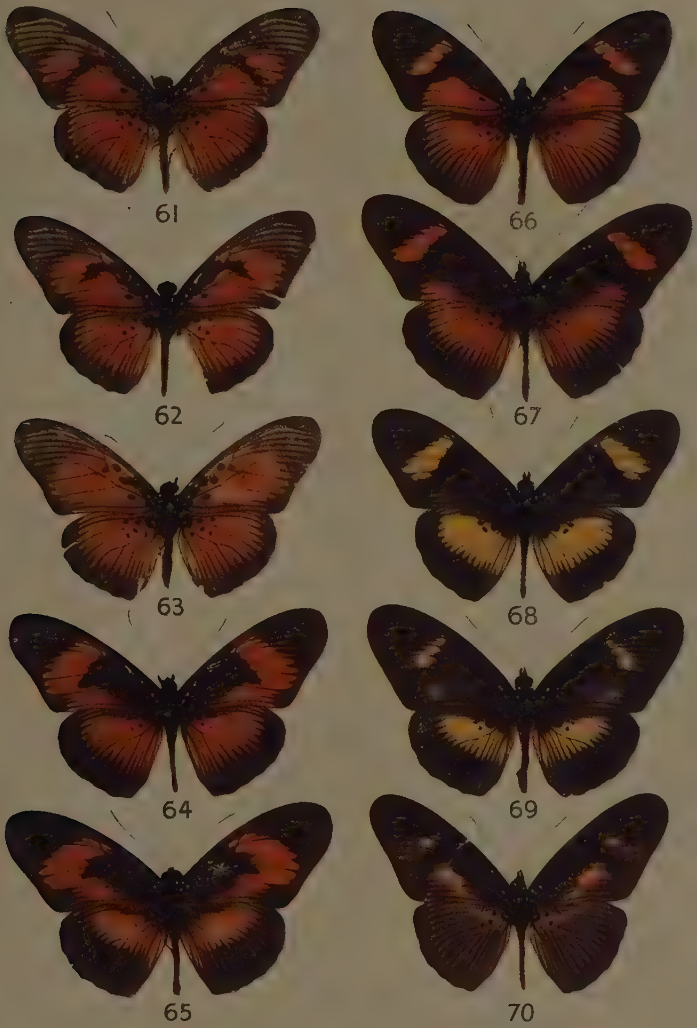
(About $\frac{5}{8}$ natural size).

PLATE VII.

Male forms of *Pseudacraea eurytus* (L.). East Africa.

FIG.

61. *rogersi* Trim., atypical. Kenya Colony, south of Mombasa, Kwale, April, 1939, T. H. E. Jackson. (Coll. Jackson.)
62. *rogersi* Trim., slightly atypical. Date as 61 except date October.
63. *rogersi* Trim., atypical. Data as 61.
64. *conradti* Oberth., atypical. Tanganyika Territory, Usambara, Amani, May, 1945, native collector for T. H. E. Jackson. (Coll. Jackson.)
65. *occidentalis* Auriv. [Tanganyika Territory.] Usigua. (B.M., Joicey bequest.)
66. *pondo* forma nova. Type. South Africa, Cape Province, West Pondoland, Port St. John's, 16th April, 1915, H. H. Swinny. (B.M.)
67. *conradti* Oberth., typical. Nyasaland, Chinteche. (B.M.)
68. *mlanjensis* Crpntr., typical. As 67, 14th May, S. A. Neave. (B.M.)
69. *imitator* Trim., typical. Natal, Durban, bred 22nd March, 1910, A. D. Millar. (O.U.M.)
70. *jacksoni* forma nova. Type. Uganda, Bugoma forest, October, 1939, T. H. E. Jackson. (O.U.M.)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Male forms of *Pseudacraea eurytus* (L.). East Africa.

(About $\frac{5}{8}$ natural size).

PLATE VIII.

Historic specimens of *Pseudacraea eurytus* (L.)

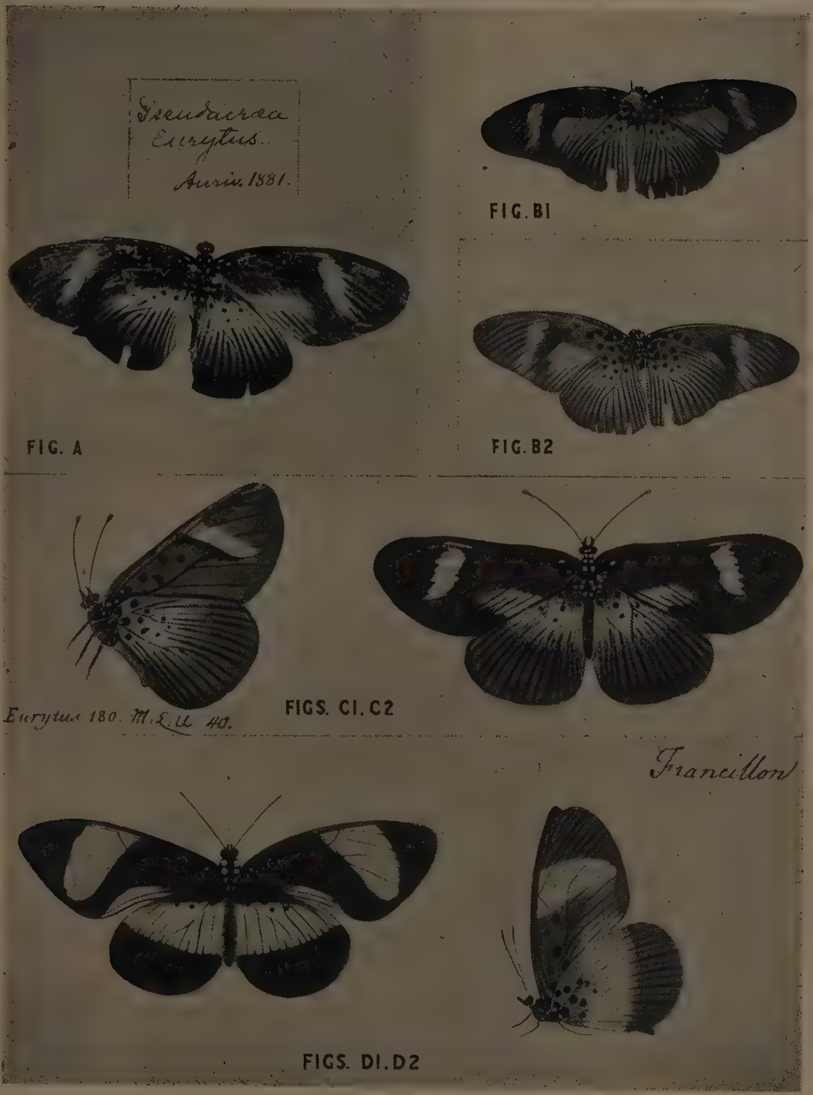
FIG.

A. The Linnaean type of *eurytus*, in the Linnaean collection, Uppsala. Photo. by kindness of Mr. W. H. T. Tams, 1947.

B. The male of *eurytus* ("*hirce*") in the Banksian collection in the care of the Linnaean Society of London. Photo. by W. H. T. Tams.

C. Clerck's figure of *eurytus*. Photo. by kindness of Bodley's librarian.

D. Figure by Jones in his "Icones." Photo. by kindness of Bodley's librarian.


Pseudacraea
Eurytus.
Auriv. 1881.
FIG. B1
FIG. A
FIG. B2
Eurytus 180. M.L.U. 40.
FIGS. C1. C2
Francillon
FIGS. D1. D2

Historic specimens of *Pseudacraea eurytus* (L.).

Adlard & Son, Ltd., Dorking.

Vol. 100. Part 4. Pp. 135–146, 3 figs. 15th June, 1949

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CONTENTS

Fraser, Lt.-Col. F. C., I.M.S. (Retd.), F.R.E.S.
The *Zygoptera* of Mauritius (Order Odonata) . 135–146, 3 figs.

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THE *ZYGOPTERA* OF MAURITIUS (ORDER ODONATA).

By Lt.-Col. F. C. Fraser, I.M.S. (Retd.), F.R.E.S.

Manuscript received 21st May, 1948.
(Read 1st December, 1948.)

With 3 Text-figures.

It is nearly eighty years since anything was published on the Zygopterous fauna of Mauritius, that is, if we except those species which have a distribution extending beyond the confines of the island, such as *Ischnura senegalensis* (Rambur) or *Pseudagrion punctum* (Rambur), the former being widely distributed from Senegal in West Africa to the Philippines, and the latter occurring in the neighbouring continent of Africa. Our knowledge of the purely endemic fauna is contained in the imperfect descriptions of the two species *insulare* Selys and *rufipes* Rambur, the generic positions of which were, and still remain to the present day, decidedly obscure. The collections made by Mr. Vinson, which have been passed on to me to deal with, have now given us ample material to clear up this obscurity and to place the taxonomy on a sound basis. The collections contain numerous examples of *insulare* and *rufipes*, as well as specimens of *Pseudagrion punctum* (Rambur) and a new species of *Ischnura* described below which I have great pleasure in naming *vinsoni*, after its collector. Mr. Vinson also informs me that he has taken another species of *Ischnura*, and although I have not yet seen this, it is safe to say that it will turn out to be *I. senegalensis* (Rambur), which has been reported already from Mauritius by Selys, but not so far included in Mr. Vinson's collections.

There remains still to be rediscovered *Platycnemis mauriciana* Selys, described in 1863, from an incomplete male, as a race of *latipes* but later (1886, *Rev. Syn. Agr.* : 223) as a possible new species. Dr. Erich Schmidt has some unpublished descriptions of species belonging to this genus from Madagascar, one of which may be *mauriciana*. It is to be hoped that Mr. Vinson will soon add this species to his now nearly complete list of the Odonata of the island.

In this paper, *Agrion insulare* Selys, whose retention in the genus *Agrion* is now obviously impossible, has been placed in a new genus : the case of *rufipes*, however, has presented greater difficulties. It was described originally by Rambur as an *Agrion* in 1842 and listed under the same genus by Selys in 1862. In 1869, Selys placed it under a new genus, *Agriocnemis*, but unfortunately gave no definition for the latter. Listed under his new genus were *solitaria* Selys (nom. nud.), *rufipes* Rambur and *exilis* Selys (nom. nud.) : thus *rufipes* was the only valid species and automatically became the genotype, although not cited as such by Selys. Three years later, Selys validated *solitaria* and *exilis* by describing them more or less fully under *Agriocnemis*, the latter species, however, with a query. No mention was made in this paper of *rufipes* nor of its relationship to the other two species. Kirby, in 1890, in the capacity of first reviser, designated *rufipes* as genotype of *Agriocnemis* and undoubtedly acted within his rights ; because of our lack of knowledge of the species, this designation has never been questioned. (Dr. Ris, however, in his private and unpublished catalogue of Odonata, quoting Kirby's reference, puts " (Type des Gattung ! !) " and omits this species altogether from his list under *Agriocnemis.*) It was not until 1877 that Selys gave the first definition of the genus *Agriocnemis*, listing under it ten species, including in this number *exilis*, but excluding *solitaria* and *rufipes* ; the former was placed in a new genus, *Argiocnemis*, the latter relegated again to its former genus, *Agrion* ! It is difficult to fathom the Selysian reasons for this *volte face*, for he had the type of *rufipes* before him in his own collection : nor can he be said to have forgotten his original reference, for he actually cites Pollen and Van Dam where *rufipes* is listed under *Agriocnemis*.

Since Selysian times, the number of species in *Agriocnemis* has risen to 26 and our conception of the genus has become a sharply-defined and fixed one, with *A. pygmaea* (Rambur), a species found in every known collection, especially typifying it. This conception and the characters of *pygmaea* and of its numerous relatives are entirely at variance with those of *rufipes*, so that, if according to the Rules of Nomenclature, the name *Agriocnemis* be reserved for the latter, it will necessitate the removal of more than two dozen species to a new genus with all the resultant chaos involved. I have discussed this problem with a number of my colleagues and we have come to the joint conclusion that it will involve less disturbance of existing nomenclature if the name *Agriocnemis* be retained for the large group *pygmaea*, whilst a new genus be erected for the comparatively little-known *rufipes*. Accordingly we have addressed the International Commission to this effect and, in anticipation of a favourable outcome to the appeal, and to avoid unnecessary delay in the preparation of this paper, I have decided to erect a new genus, *Coenagriocnemis*, to accommodate *rufipes* : for *insulare*, which now stands under *Agrion*, a second new genus, *Coenargiocnemis*, is erected. These two names, nearly approaching those of the old, are easily assimilated and will thus cause less confusion in the nomenclature. The late Mr. J. E. H. Roberts has suggested that *exilis* be chosen as the new genotype for *Agriocnemis*, and I was at first inclined to agree with this proposal since it was one of the three species originally included under the genus by Selys, but *exilis* is less well known than many of the other species and it was also described from an imperfect specimen with the end of the abdomen missing and therefore without anal appendages. Since these appendages are the principal character for differentiating the species and since, therefore, it is by no means certain that what is now known as *exilis* is synonymous with the Selysian type, it seems to be more practical to choose a species of which there is no doubt and which is well known to all specialists in the order : I therefore designate *Agrion pygmaea* Rambur as the genotype of *Agriocnemis* Selys.

Only seven species of Zygoptera are known from Mauritius and all of these belong to the smaller species of the superfamily *Coenagrioidea*. These are classified as follows :

Family Coenagriidae.

Genus *Ceriagrion* Selys.

1. *C. glabrum* (Burmeister).

Genus *Pseudagrion* Selys.

2. *P. punctum* (Rambur).

Genus *Ischnura* Charpentier.

3. *I. senegalensis* (Rambur).
4. *I. vinsoni* sp. n.

Genus *Coenagriocnemis* gen. n.

5. *C. rufipes* (Rambur).

Genus *Coenargiocnemis* gen. n.

6. *C. insulare* (Selys).

Family Platycnemididae.

Genus *Platycnemis* Charpentier.

7. *P. mauriciana* Selys.

Key to Species of the Mauritian Zygoptera.

1. Ground-colour white with strongly contrasted black markings; tibiae markedly and fusiformly dilated . . . . *Platycnemis mauriciana* Selys.
Ground-colour other than white; tibiae not dilated . . . . 2.
2. Species uniformly coloured orange and without any trace of dark markings; females uniformly olivaceous . *Ceriagrion glabrum* (Burm.).
Species with blue ground-colour and extensive dark markings . . . 3.
3. Dorsum of thorax black, marked with two bright brick-red stripes; superior anal appendages with crochet-hook-like apex; apex of segment 10 without tubercles . . . . *Pseudagrion punctum* (Rambur).
Dorsum of thorax black, marked with blue or greenish-yellow stripes; superior anal appendages variable but usually with a robust ventral spine; two small tubercles separated by a notch on the apical border of segment 10 . . . . 4.
4. Pterostigmas of fore and hind wings differing in colour . . . . . 5.
Pterostigmas of fore and hind wings of the same colour . . . . . 6.
5. Superior anal appendages without a ventral spine; inferior anal appendage sloping strongly upwards; segment 9 black on dorsum *Ischnura senegalensis* (Rambur).
Superior anal appendages with long curved ventral spine; inferior anal appendages directed straight backwards; segment 9 blue on dorsum *Ischnura vinsoni* sp.
6. Legs bright chrome yellow; blue antehumeral stripes, complete and flanked outwardly by a second much finer stripe *Coenagriocnemis rufipes* (Rambur).
Legs black; blue antehumeral stripes broadly interrupted, forming an upper isolated spot and a lower wedge-shaped stripe broadest inferiorly . . . . *Coenargiocnemis insulare* (Selys).

Ceriagrion glabrum (Burmeister).

Agrion glabrum Burmeister, 1839, *Handb. Ent.* **2** : 821.
Agrion ferrugineum Rambur, 1842, *Ins. Nevrop.* : 280.
Brachybasis glabra Selys, 1869, *Ann. Soc. ent. Belg.* **12** : 95.
Telebasis glabrum Selys, 1869, *Pollen and Van Dam, Madagasc. Ins.* : 24.
Ceriagrion glabrum Selys, 1876, *Bull. Acad. Belg.* (2) **42** : 527. (Mauritius.)
Brachybasis rhomboidalis Kirby, 1898, *Ann. Mag. nat. Hist.* (7) **2** : 245.
Ceriagrion rhomboidalis Grünberg, *Zool. Jb.* (*Syst.*) **18** : 699.
Ceriagrion glabrum Campion, 1914, *Ann. Mag. nat. Hist.* (8) **14** : 277. (Mauritius and Madagascar.)
Ceriagrion glabrum Fraser, 1941, *Proc. R. ent. Soc. Lond.* (B) **10** : 62. (Key to African species of genus.)

Material examined: 3 males from Moka, 10.vi.45, coll. J. Vinson. The species is widely distributed throughout Africa and Madagascar, and has extended as far eastwards as the Seychelles and Mauritius. Easily distinguished from all other Mauritian species of *Coenagrion* by its bright orange colouring without any dark markings, and from all other species of the same genus by the robust spines flanking the deep apical notch on segment 10.

Pseudagrion punctum (Rambur). (Fig. 1, *f* and *g*).

Agrion punctum Rambur, 1842, *Ins. Nevrop*: 260.

Agrion punctum Selys *in* Maillard, 1862, *Annexe K. Nevrop.*: 35 (Réunion, Bourbon).

Agrion punctum Selys, 1869, *Pollen and Van Dam, Madagasc. Ins.*: 24. (Madagascar.)

Agrion ? punctum Selys, 1876, *Bull. Acad. Belg.* (2) **41**: 1291 (*Syn. Agr.* (sep.): 181). (Mauritius.)

Coenagrion punctum Kirby, 1890, *Cat. Odon.*: 150.

Pseudagrion punctum Gerstaecker, 1891, *Jb. Hamburg. Wiss. Aust.* **9**: 8 (sep.) (Female described.)

Pseudagrion punctum Forster, 1906, *Jahrb. Nassau.* **59**: 338. Forster, 1906, *Jahrb. Mannheim* **71–72**: 59.

Pseudagrion punctum Ris, 1908, *Jenaische Denkschr.* **13**: 315.

Pseudagrion punctum Ris *in* Schmidt, 1936, *Abh. senkenberg. Naturf. Ges.* **433**: 4, 8, 9, 13 (key), 15 (key), 47.

Material examined: 7 males and 3 females, Moka, ii.45, 9.x.46, 21–31.xii.46 and 4.ii.47. (Examples from Madagascar have also been examined.) Only four are fully adult and these have the pale areas of the head, thorax and prothorax a bright brick-red on the dorsum, pale blue on the sides: all others are pale blue or a light greyish with black markings. Behind the head is broadly pale except for some black in the occipital foramen area. The mid-dorsal blue spot on segment 2 is variable in size and oval or cordate in shape: segments 8–10 are entirely blue in the male. The dorsal marking of segment 2 in the females is dagger-shaped with the hilt of the dagger at the apical end. The anal vein leaves the border of the wing well proximal to the level of Ac: postnodals number 12–13 in the fore-wings, 10–11 in the hind. The superior anal appendages differ from others in the genus by sloping strongly upwards and outwards, ending in a small crochet-like hook.

Ischnura senegalensis (Rambur). (Fig. 1, *d*.)

Agrion senegalensis Rambur, 1842, *Ins. Nevrop.*: 276.

Agrion senegalensis Selys, 1869, *Pollen and Van Dam, Madagasc. Ins.*: 24. (Madagascar and Mauritius.)

Agrion senegalensis Selys, 1850, *Rev. Odon.*: 186.

Ischnura senegalensis Selys, 1876, *Bull. Acad. Belg.* (2) **41**: 273.

Micronympha senegalensis Kirby, 1890, *Cat. Odon.*: 141.

Ischnura senegalensis Fraser, 1933, *Fauna Brit. Ind.* (*Odon.*) **1**: 348. (Redescription of both sexes.) (Ris cites some 68 references to this widely distributed species in his private catalogue.)

Material examined: Mr. Vinson has not sent this species but has recently informed me that he has taken another species besides the new *Ischnura vinsoni* described below. I think there can be little doubt that his second species is *senegalensis* which has been reported already from Mauritius by Selys. The figures given in this paper will serve to differentiate it from *I. vinsoni*. *Senegalensis* is remarkable for its dominant character, for which its adaptability to all altitudes from sea-level to over 7,000 ft. and to climates from the wettest to the most arid is the most probable reason : it is, in fact, a palaearctic species which has adapted itself to tropical conditions. It has been reported from localities as wide apart as Senegal and the Philippines.

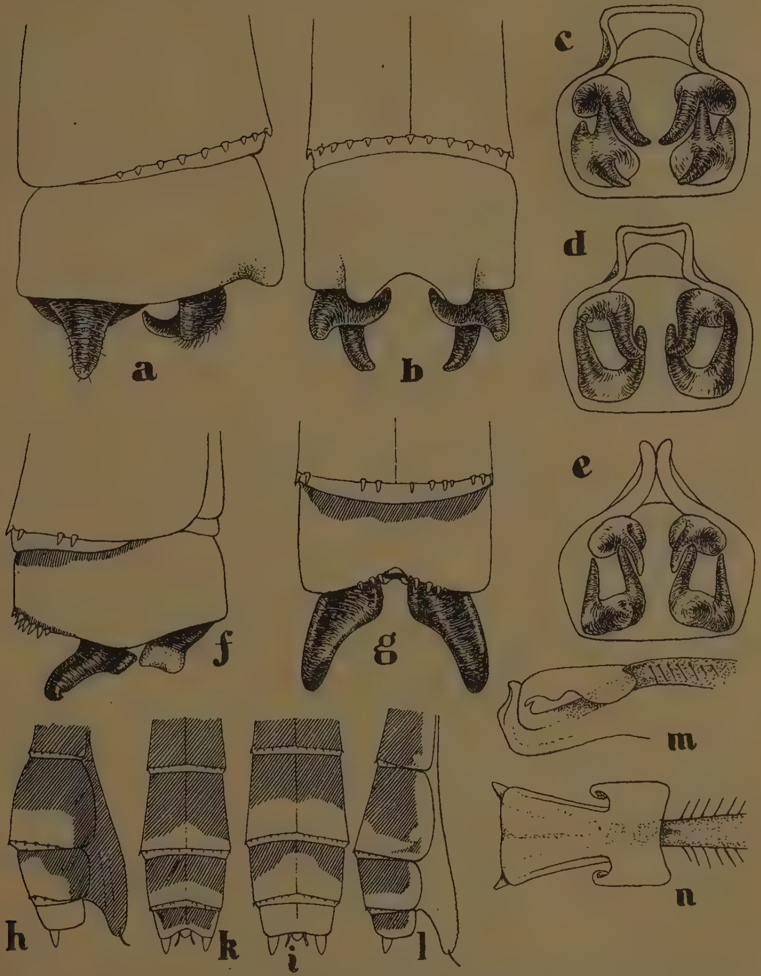

FIG. 1.—*a* and *b*, Anal appendages of *Ischnura vinsoni* sp. n. seen from the left side and dorsum ; *c*, *d* and *e*, anal appendages viewed from the rear of *Ischnura vinsoni* sp.n., *Ischnura senegalensis* (Rambur) and *Ischnura filosa* Schmidt (Madagascar) ; *f* and *g*, anal appendages of *Pseudagrion punctum* (Rambur), seen from the right side and dorsum ; *h* and *i*, markings of abdominal segments 8, 9 and 10 of *Coenargiocnemis insulare* (Selys), female ; *k* and *l*, the same of *Coenagriocnemis rufipes* (Rambur) ; *m* and *n*, penis of *Coenargiocnemis insulare* (Selys), lateral and dorsal views.

Ischnura vinsoni sp. n. (Fig. 1, *a*, *b* and *c*.)

Material examined : 2 adult males, one with the end segments of abdomen missing, 12.i.47 ; 1 subadult female, 12.xii.46, all from Moka, coll. J. Vinson.

Male : Abdomen 23 mm. ; hind wing 15 mm.

Head : Labium straw-coloured ; labrum pale blue, broadly black at base ; anteclypeus bluish green as also bases of mandibles, genae and a transverse stripe across the frons ; postclypeus glossy black. Rest of dorsum of head black with moderately large, round, azure blue postocular spots. Beneath head greyish white save for the black occipital pit. Prothorax black on dorsum, blue laterally, this colour extending on to dorsum of anterior lobe and less so on the posterior ; the latter trilobate, the middle lobe projecting somewhat. Thorax black on dorsum marked by moderately broad pale blue antehumeral stripes which taper slightly above. Laterally pale blue with a short black line on the anterior suture and a more pronounced one on the posterior, which becomes lineate below and forks at the level of the spiracle ; pale blue on ventral surface. Legs pale creamy yellow, the femora on extensor surface and the tibiae on flexor black. Wings hyaline ; 11 postnodals in fore-wings, 9 in the hind ; pterostigma narrow and elongate, very acute at both ends, covering one cell, its proximal two-thirds black, the distal third a beautiful sky-blue. In the hind wing the pterostigma less acute at the ends and entirely black save for a fine golden yellow encircling line separating the framing nervures from the central black core. Abdomen black on dorsum, bluish laterally on the basal segments but chrome yellow thereafter ; segment 1 with a quadrate dorsal black spot extending from end to end ; segment 2 steely blue black on dorsum, but this dark area constricted subapically before becoming confluent with an apical black ring ; segments 3 to 6 with narrow basal rings of yellow interrupting the dorsal black ; segment 7 entirely black ; 8 and 9 entirely azure blue save for a narrow ventro-lateral black stripe ; segment 10 black, its apical border emarginate and presenting a short rounded tubercle on each side of the shortly rounded notch. Anal appendages black ; superiors seen from above are conical and with a very robust spine or hook extending inwards and downwards from its medial side ; laterally the body of the appendage is subquadrate and with the hook projecting downwards and a little recurved anteriorly at its apex ; the inferior appendages considerably longer, but not as long as segment 10, broadly conical as seen in profile, but narrowly spine-like in dorsal view and curved strongly inwards in a forcipate manner.

Female : Abdomen 24·5 mm. Hind wing 16·5 mm.

Simulating the male closely in markings but the ground colour pale ochraceous ; the pale stripe on frons broader, the black of vertex extending only to level of antennae. The lateral black stripes of thorax narrower ; legs yellow with a black line on the external sides of femora and tibiae. Wings hyaline ; 11 postnodals in fore-wings, 9 to 10 in the hind ; pterostigma olivaceous in all wings narrowly framed in black. Abdomen similar to the male but segment 2 glossy black, segment 8 with only its basal half to two-thirds blue, the apex black, the black broader mid-dorsally than apically ; segment 9 blue but with its base narrowly ringed with black ; segment 10 appears to be entirely black as in the male. Anal appendages black, shortly conical ; vulvar scales very robust, pale, extending to end of abdomen.

This new species which has a marked resemblance to *senegalensis* is easily differentiated by the entirely different formation of its anal appendages. The *type* and allotype will go to the British Museum.

Coenagriocnemis gen. n.

Medium sized with very slender and elongated abdomen. Wings with close venation made up mainly of quadrangular cells ; arculus situated opposite the distal antenodal ; anal vein leaving the posterior border of wing proximal to the level of *Ac* at a distance *less* than the length of *Ac*, which latter cross-vein lies nearer the distal than to the proximal antenodal; postnodals in fore-wing numbering not more than 14; costal side of quadrilateral in fore-wing only slightly longer than the base, but about twice as long as the base in the quadrilateral of hind wing; labium with a wide cleft extending for one-third of its length; hind femora with two rows of 5 tc 7 robust spines of approximately equal length;

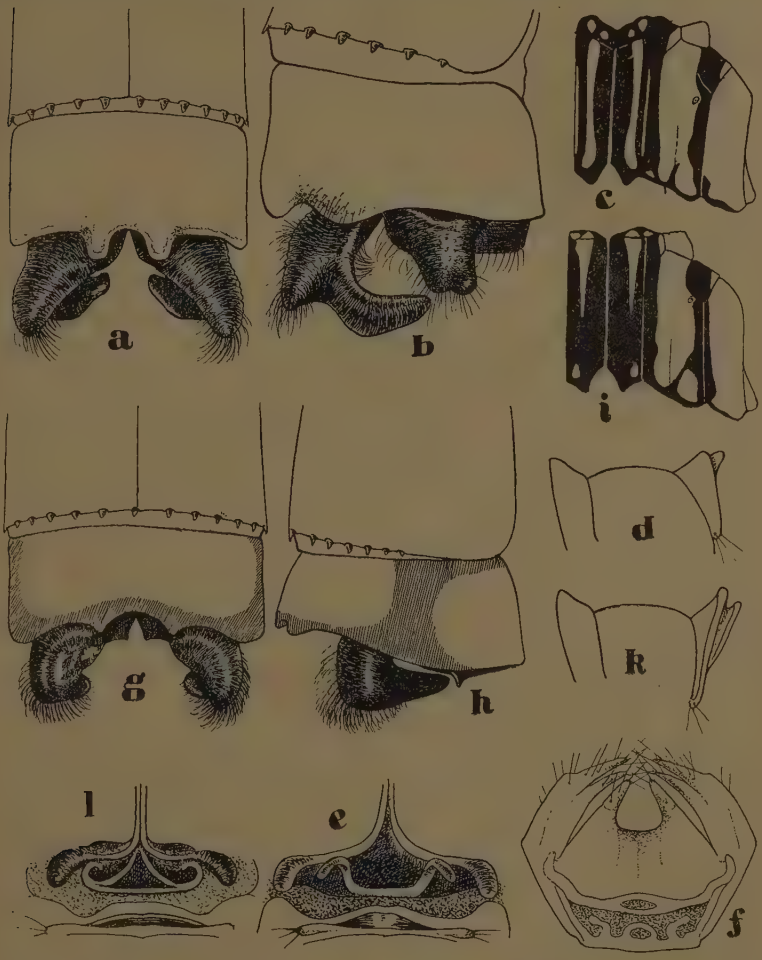

Fig. 2.—*a* and *b*, Anal appendages of *Coenargiocnemis insulare* (Selys), dorsal and right lateral views; *c*, thoracic markings of *Coenagriocnemis rufipes* (Rambur); *d*, prothorax of the same species, left side; *e*, mesostigmal lamina of the same; *f*, labium common to both *Coenargiocnemis insulare* and *Coenagriocnemis rufipes*; *g* and *h*, anal appendages of *Coenagriocnemis rufipes* (Rambur), dorsum and right side; *i*, thoracic markings of *Coenargiocnemis insulare*; *k*, prothorax of the same species seen from the left side; *l*, mesostigmal lamina of the same species.

segment 10 with a short shallow notch at its apical margin flanked by a small tubercle on each side; inferior anal appendages of male obsolete or very inconspicuous.

Genotype.—*Agrion rufipes* Rambur.

Coenagriocnemis rufipes (Rambur). (Fig. 2, *c*, *d*, *e*, *g* and *h*, Fig. 3, *a*.)

Agrion rufipes Rambur, 1842, *Ins. Nevrop.* : 256.
Agrion ? mauritianum Selys, 1862, *L. Maillard, Annexe K, Nevrop.* : 35.
Agrion ? rufipes Selys, 1862, *Id.* : 35.
Agriocnemis rufipes Selys, 1869, *Pollen and Van Dam, Madagasc. Ins.* : 24. (Mauritius.)
Agrion ? mauritianum Selys, 1872, *Rev. Zool. Guérin-Méneville* : 180.
Agrion ? rufipes Selys, 1876, *Bull. Acad. Belg.* (2) **41** : 1290. (*Syn. Agr. 5me Leg.* (sep.): 180.)
Agriocnemis rufipes Kirby, 1890, *Cat. Odon.* : 159.

Material examined: 12 males and 6 females, 10.xii.46 to 14.i.47, coll. J. Vinson, all around Moka.

Male: Abdomen 30–31 mm. Hind wing 18 mm.

Head: Labium straw-coloured; labrum bright or pale yellow or pale olivaceous in some with the basal three-fourths dark olivaceous; bases of mandibles, genae, anteclypeus and a narrow transverse stripe across the frons bright chrome or ochreous; postclypeus glossy black; rest of head, including vertex, occiput and beneath black, the latter, in adults, thinly whitish pruinose and the occiput bearing rather large azure blue cordate postocular spots. Prothorax black on dorsum, citron yellow low down on the sides and prolonged finely across the anterior lobe; posterior lobe broadly rounded, with a sulcus throwing it into two ridges and with 3 bristles projecting from each outer end. Thorax black on dorsum, this colour extending laterally to cover the anterior third of mesepimeron, marked by a fine greenish yellow incomplete humeral line and narrow complete greenish or bluish-green antehumeral stripes which are continuous with the yellow on the sides of prothorax. Laterally bluish-green or greenish with a point of black on the first lateral suture and a complete narrow black stripe on the second which passes under the pectus to become confluent with the stripe from the other side; this stripe and the black on the anterior part of mesepimeron thinly pruinose in adults giving a bluish appearance to these areas. Beneath yellow with two large black pyriform spots confluent medially in the greater part of their length. Legs bright ochreous (not red as the name would imply, but more of a tangerine orange in colour), with a black point at the outer and distal end of each femur, the first segment of the tarsi as well as the claws also black. Wings hyaline; 14 postnodals in fore-wings, 11–12 in the hind; pterostigma diamond-shaped, rather more acute distally, covering slightly less than one cell, reddish ochreous with blackish centre and black framing nervures, of the same size and shape in all wings. Abdomen glossy black on dorsum, bluish on the sides of segments 1 and 2, and basal part of 3, the dorsal black on segment 2 shaped as a narrow thistle-head, that on segments 3 to 7 extending from end to end of segments, but the pale colour of sides passing up at the base of each segment to form small paired basal spots; segments 8 to 10 entirely azure blue on dorsum, 8 and 9 narrowly black ventro-laterally and 10 with a narrow black stripe at its middle height. Anal appendages black: superiors seen from above are broadly conical and nearly as long as segment 10, they are shallowly hollowed out on the inner aspect and thickly coated with stiff golden yellow hairs at the apex; laterally they are sharply angulated due to a broad triangular plaque extending from the inner side downwards and inwards. Inferior appendages very inconspicuous, broad mammilated processes with a nipple-like apex just projecting from the apical end of the segment.

Female: Abdomen 28–30 mm. Hind wing 19 mm.

Head, thorax and legs similar to the male, but the legs, in full adults, a duller ochreous and the ends of femora and tibiae a little infuscated; the abrum with the base darker; wings with 13 to 14 postnodals; pterostigma rather more elongate, olivaceous with black centre and framing nervures. Abdomen variably coloured according to age and largely bright ochreous from segment 1 to 5 in the subadult with black markings beginning to appear on the dorsum as narrow subapical rings. Adults with broad dorsal markings from segment 1 to 7, bright ochreous laterally, segments 8 to 10 blue, 8 with its basal two-thirds black, 9 with about its basal half black but the sides blue, whilst 10 has the ventro-lateral border and apex of dorsum blue. Anal appendages very shortly conical; vulvar scales robust, just overlapping the end of abdomen, pale. (In some subadult females, the dorsal black of abdomen on the first five segments consists of narrow apical rings and narrow mid-dorsal stripes which dilate subapically and are again constricted before joining the apical rings). There is no ventral spine beneath segment 8, but the general facies of this species suggests an origin from an Ischnurine ancestor.

Coenargiocnemis gen. n.

Comparatively large and robust. Wings with very close venation made up mainly of quadrangular cells; arculus situated opposite the distal antenodal; anal vein in fore-wing leaving the posterior border of wing proximal to the level of *Ac* at a distance *greater than* the length of *Ac* and at a point much nearer the proximal antenodal than the distal one; *Ac* situated at a point midway between the two antenodals; postnodals in fore wing numbering from 18 to 19; costal side of quadrilateral in fore wing generally of the same length as the base; in the hind wing variably twice the length or only half as long again (both in the fore and hind wings, these cells are remarkably variable, thus in the two hind wings of one specimen, the costal side of the cell is half as long again in the right wing and about three times as long in the left. Similar aberrations are found in other specimens). Labium with a wide cleft extending for one-third of its length; hind femora with about 8 robust spines which gradually lengthen from base to distal end; a second inner row of about 12 short robust spines of equal length throughout; segment 10 with very short, very deep notch which is flanked by prominent rounded tubercles. Anal inferior appendages broadly conical and projecting horizontally conspicuously and nearly as long as the superiors.

Genotype: *Agrion insulare* Selys.

Coenargiocnemis insulare (Selys). (Fig. 2, *a*, *b*, *f*, *i*, *k*, and *l*; Fig. 3, *b*).

Agrion insulare Selys, 1869, *Pollen and Van Dam, Madagasc. Ins.*: 24. (Mauritius, Bourbon.)

Agrion ? insulare Selys, 1872, *Rev. Mag. Zool.*: 179.

Agrion ? insulare Selys, 1876, *Bull. Acad. Belg.* (2) **41**: 1288. (Réunion, Mauritius) (*Syn. Agr.* 5me *Leg.* (sep.): 178).

Coenagrion insulare Kirby, 1890, *Cat. Odon.*: 150.

Agrion insulare ? Calvert, 1895, *Proc. U.S. nat. Mus.* **18**: 142. (A male with end of abdomen absent, Seychelles.)

Material examined: 1 pair, G.B., 10.xi.45; 1 female, Curepipe, 3.i.43; 1 pair, 10.xii.46; 2 males, 12.xii.46; 1 male, 0.xii.46; all coll. J. Vinson, in the Moka District. 1 pair, Reduit, Mauritius, 4.ii.47, coll. Ray Ramet.

Male: Abdomen 36–37 mm. Hind wing 24–25 mm.

Head: Labium straw-coloured; labrum and postclypeus glossy black, the former narrowly bordered with pale yellow anteriorly; bases of mandibles, genae, anteclypeus and a narrow stripe across frons interrupted medially, all citron yellow; vertex and occiput black, the latter with rather small azure-blue rounded postocular spots; antennae black ringed with reddish brown; beneath head black. Prothorax broadly steely black on dorsum and upper part of sides; a transverse line on the anterior lobe and a small spot at each outer end of the posterior lobe, as well as the lower part of sides bluish. Thorax steely or bronzed black on dorsum to as far lateral as the anterior half of mesepimeron marked by intèrrupted antehumeral stripes which are very broad below but rapidly taper away until lost at about halfway up the dorsum; in all but full adults, there is an upper humeral spot of blue representing the upper end of the antehumeral stripe. Laterally bluish above adjacent to the black but then passing to bluish green and finally pale yellow below and beneath. An oblique black line starting from the first suture and running back to meet or nearly meet a broad complete black stripe on the postero-lateral suture. Beneath, two large black pyriform spots broadly confluent in nearly all their length, but entirely concealed beneath dense pruinescence. Legs rather short and robust, black save the flexor surface of all femora which are pale yellow overlaid with white pruinescence. Wings hyaline; pterostigma narrow and elongate, very acute at both ends, bright golden brown with slightly darker centre and black surrounding nervures, covering from 1 to 2 cells; 18–19 postnodals in fore-wings, 16–17 in the hind. Abdomen black dorsally from segment 1 to 7, segments 8 to 10 entirely azure blue. Segment 1 broadly blue on the sides, segment 2 with a broad oval lateral blue spot constricting the dorsal black on each side, and a pair of blue apical lunules; segments 3 to 6 with small basal paired spots of blue, rather larger and elongate on 3, but becoming almost obsolete on the following segments; the lower parts of the sides of all segments from 2 to 7 bright chrome yellow. Anal appendages black; superiors seen from above broad divaricate conical processes with a very large and robust process showing partially on the inner side; this process,

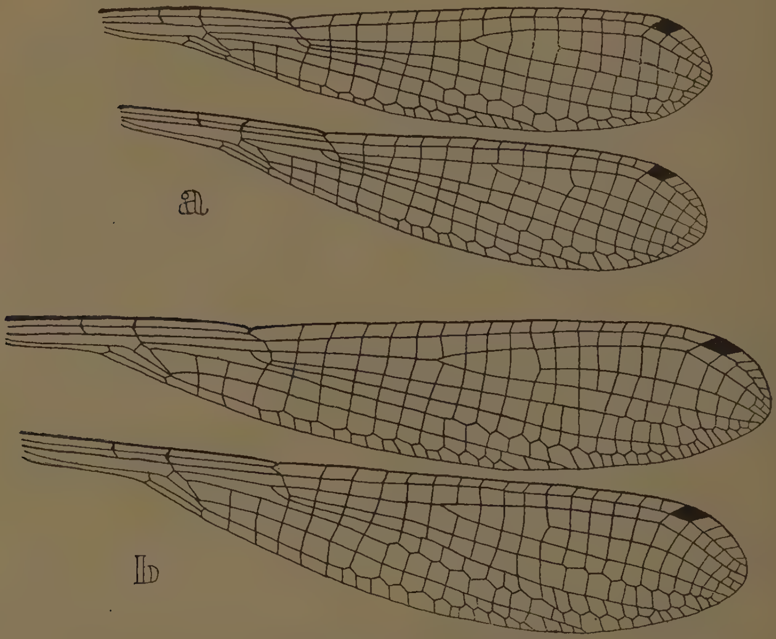

Fig. 3.—Wings of (*a*) *Coenagriocnemis rufipes* (Rambur); (*b*) *Coenargiocnemis insulare* (Selys).

seen in profile, is strongly curved downwards and inwards, giving a hasp-like shape to the whole appendage. Inferior appendages broad conical processes slightly bifid at apex projecting straight posteriorly and about two-thirds the length of superiors.

Female : Abdomen 37 mm. Hind wing 28 mm.

Exactly similar to the male in colour and markings save for segments 8 and 9, the former black with a broad pale blue stripe covering its apical half or slightly less, the latter with rather more than its apical half blue but subject to some variation ; segment 10 with its sides black, dorsum blue. Vulvar scales black, extending to end of abdomen, very robust. Wings hyaline, pterostigma olivaceous ; 18 postnodals in fore wings, 16 in the hind.

It will be seen from the definitions of the genera *Coenagriocnemis* and *Coenargiocnemis* and the descriptions of the two species, *rufipes* and *insulare*, that many points of contact exist between them ; indeed the significance of some of these is so great that I have hesitated before placing the two species in different genera. However, even if they be not congeneric, the evidence is overwhelmingly in support of their having taken origin from a common ancestor and that we see in these two species the genesis of a number of insular forms comparable with the Megalagrions of Hawaii, the Ischnuras of Samoa or the Platystictas of Ceylon.

Rufipes and *insulare* agree in the widely cleft labium, the rather similar shape of the posterior lobe of the prothorax, the general shape of the superior anal appendages, the presence of apical tubercles on segment 10, the presence of postocular coloured spots, the absence of a ventral spine to segment 8 and the quadrangular nature of the venation of the wings. A minor but, I think, significant character shared by the two species is the presence of two unusual black confluent pyriform spots on the pectus of the thorax.

The most important points of disagreement are the slim and brightly coloured legs of *rufipes*, contrasted with the rather short, robust black legs, with different armature, of *insulare* ; the shorter petiolation of the wings in *insulare* and the greater development of the apical tubercles on segment 10 in the same species. The great disparity in size is not in itself very important, as great variation in this respect is also found in the Megalagrions.

Platycnemis mauriciana Selys.

Platycnemis mauriciana Selys, 1862, *Annexe K. Nevrop.* : 35, *in* Maillard. (*Notes sur L'Ile de la Réunion et Bourbon*), Paris.

Platycnemis mauriciana Selys, 1869, *Pollen and Van Dam, Madagasc. Ins.* : 10 (as *latipes* var.)

Platycnemis mauriciana Selys, 1863, *Bull. Acad. Belg.* (2) **16** : 167. Selys, 1886, *Mem. Cour. Soc. ent. Belg.* **38** : 223.

The type, an incomplete male, is the only specimen known and was in the Serville collection, indicated from Mauritius, a locality which Selys queried. In view of the fact that several species are known from Madagascar, it is exceedingly probable that the specimen was labelled correctly in this case, in spite of the unreliability of the Serville data. The short description is closely similar to that of *P. hova* Martin from Madagascar, and if not that species, it is certainly closely related to it.

ADDENDA

Since the above was written, Mr. Joseph Vinson has sent me much more material which includes the second species of *Ischnura*, of which he had made mention ; this proves to be *I. senegalensis* (Rambur), as I had surmised. There are 7 males, 1 heteromorphic and 4 andromorphic females, two of the latter being still *in cop.* with the males and thus affording the best of proofs that they are related. The male differs somewhat from type by the antehumeral stripes either very finely delineated, partially interrupted or absent altogether. Both sexes have only from 8 to 9 postnodal cross-veins in the fore-wings as compared to 11 or 12 in *vinsoni*, this fact offering an easy method for differentiation of the two species. Over 40 males and 24 females of *vinsoni* have been sent and it is now seen that, in the female, segments 8 to 10 are entirely black dorsally. The blue markings noted in the original description are apparently artifects. The ground-colour of the head and thorax for the females is a rich orange, becoming infuscated in the very old specimens.

Of the remaining species, 4 pairs of *P. punctum* (Rambur), 4 pairs of *C. insulare* (Selys) and 7 males and 4 females of *C. rufipes* (Rambur) are contained in the new material and offer no fresh information.

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CONTENTS

PAGE
Waloff, N., Ph.D., F.R.E.S. Observations on larvae of *Ephestia elutella* Hübner (Lep. Phycitidae) during diapause . . . . . . 147–159, 1 fig.

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OBSERVATIONS ON LARVAE OF *EPHESTIA ELUTELLA* HÜBNER (LEP. PHYCITIDAE) DURING DIAPAUSE.

By N. Waloff, Ph.D., F.R.E.S.

(*Department of Zoology and Applied Entomology, Imperial College, London.*)

(With One Text-figure.)

Manuscript received 17th April 1948.

Read 1st December, 1948.

1. Introduction.

There is one main generation of *Ephestia elutella* in this country. The maximum flight of moths is at the end of June and in the first half of July. This is followed by a very small second generation, which numerically is only one-sixtieth to one-seventieth of the first and partly overlaps it. Reed and Livingstone (1937) record three generations in Richmond, Virginia, and Ustinov (1932) speaks of three possible generations in Abkhasia. In this country the fully fed larvae wander for a few days and then spin up in cracks and crevices. The period of quiescence lasts 8–9 months and then the larvae begin to pupate in April or May of the following year.

2. Dissections of the Diapausing Larvae.

The diapausing larvae are not completely inactive, but metabolize slowly and produce excretions throughout the period of quiescence. The faeces are eliminated in the wandering period of the fully grown larvae or at the time of spinning of the coccon, but excretions from the Malpighian tubes are produced at the time of spinning, at irregular intervals throughout the period of diapause and finally, in larger quantities, before pupation. At first these excretions are bright orange and semi-fluid, but on drying they become brown and crystalline. Arseno-tungstic acid test shows that they contain uric acid.

Samples, each of 50 larvae, from outdoor temperatures were dissected in November, 1944, and in January, February, April and May, 1945 (Table I). At no stage in diapause was the gut empty in all the dissected larvae and, in a few of them, it was completely full of excretions. It was noted that, generally, the pinkish colour of the Malpighian tubes was an indication of the small crystalline granules in their lumina. In April, the tubes appeared white and opaque. This opacity was caused by small white particles in the fluid contents of the tubes and coincided in time with the " broken-up " or exhausted appearance of the fat body in many of the larvae. The fat body was somewhat arbitrarily classified as large, medium or small. By April it was definitely smaller in many of the larvae.

TABLE I.—*Dissections of Samples of* 50 *Diapausing Larvae kept at Outdoor Temperatures.*

Date.	Gut.					Fat body.	Malpighian tubes.
	Empty.	Full.					
		Whole length.	Fore.	Mid.	Hind.		
29.ix.44	29	1	1	13	6	7 large, 3 small (others not noted)	11 pink 39 transparent
12.i.45	33	4	3	3	7	17 large 14 medium 19 small 7 exhausted	3 pink 47 transparent
10.ii.45	35	9	3		3	8 large 19 medium 23 small 6 exhausted	20 pink 30 transparent
16.iv.45	24	18	4		2*	6 large 14 medium 30 small 19 exhausted	0 pink 24 opaque 26 transparent
v.45	30	16	–	–	4	14 large 16 medium 20 small 38 exhausted	18 pink 2 opaque 30 transparent

* Only 48 recorded.

3. THE WATER CONTENT, FAT CONTENT AND THE LOSS OF WEIGHT IN THE DIAPAUSING LARVAE.

In 1943–44 the water content and the average weights of the diapausing larvae were determined. More frequent determinations were made in 1944–45, when the total fat was also extracted in ether in a Sohxlet. The water content was determined by heating samples of 25 larvae at 110° C. for 3 hours. The results of these determinations are set out in Tables II and III, where it can be seen that the water content first falls in the diapausing larvae and is then retained at a fairly constant level in spite of the progressive loss of weight. It again rises slightly at the termination of this period.

TABLE II.—*The Average Weights and Water Contents of Larvae Diapausing in Unheated Conditions.*

1943–44.

Date of collection.	Number of larvae.	Average weight. mg.	Per cent. water content (wet weight).
16.ix.43	150 wandering	17·6	–
29.ix.43	202 ,,	16·4	–
7.x.43	196 ,,	15·5	–
15.ii.44	465 spun up	12·9	59·1
15.iii.44	400 ,,	13·8	58·7
14.iv.44	250 ,,	10·8	57·5
11.v.44	250 ,,	10·9	60·5
26·v.44	134 ,,	10·7	60·0
6.vi.44	42 ,,	9·9	60·2
15.vi.44	16 ,,	10·6	62·0

1944–45.

Date of collection.	Number of larvae.	Average weight mg.	Per cent. water content (wet weight).
1.ix.44	213 wandering	14·9	63·9
29.ix.44	200 ,,	11·6	61·1
13.x.44	500 spun up	11·3	62·5
3.xi.44	175 ,,	9·7	59·5
8.xii.44	225 ,,	10·3	59·9
5.iii.45	300 ,,	10·1	59·8
11.iv.45	300 ,,	9·4	61·3
22.v.45	175 ,,	8·5	61·0
31.v.45	80 ,,	9·1	62·0

TABLE III.—*Total Fat Content Expressed as Percentage of Dry Weight.*

Date.	xi.1944.	xii.44	i.45.	iii.45	iv.45.	v.45.
Number of sets of 300 larvae . . .	3	1	3	1	2	1
Total fat content (per cent. of dry weight)	47·5	50·4	44·3	45·1	43·4	40·8

At the beginning of diapause the lighter larvae have a higher water content than do the heavier ones. Thus, on the 1.ix.44 the 200 selected small larvae of 9·1 mg. average weight had 65·5 per cent. water content, whereas 213 heavier larvae of 14·9 mg. average weight had 63·9 per cent. water of live weight. As the originally heavier larvae tend to survive the winter and the lighter ones die out (Richards and Waloff, 1946), the fall in the water content of the diapausing larvae may be, at least partly, due to the differential mortality, i.e. to the elimination of the originally lighter sections of the population.

The loss in weight of the diapausing larvae is both continuous and considerable. Some of it may be accounted by the direct evaporation from the body, as was seen on keeping weighed larvae at 90 per cent. R.H. and at 40 per cent. R.H. at room temperature (Table IV). However, there is little doubt that most of it is the result of slow metabolic changes indicated by the decrease of the total fat content of the larvae from 47·5 per cent. of dry weight in November to 40·8 per cent. in May, by the general broken-up appearance of the fat body (which is also a store of protein, Wigglesworth, 1939) by April and by the slow, continuous elimination of nitrogenous waste in watery solution through the Malpighian tubes. The total loss of weight is considerable and in 1943–44 it was from 16·4–17·6 mg. in September to 10·8 mg. in April. The corresponding loss in 1944–45 was from 14·9 to 9·4 mg. Table V shows the progressive loss in weight of individual larvae kept in an unheated outhouse in a desiccator with KOH at 70 per cent R.H.

Table IV.—*Diapausing Larvae Transferred to* 40 *per cent. R.H. and* 90 *per cent. R.H. at Room Temperature and Weighed Weekly,* 29.i–26.ii.45. (*Pupated within* 5–7 *weeks.*)

Number of larvae.	Relative humidity.	Average weight (mg.).			
		1st.	2nd.	3rd.	4th week.
29	40%	11·39	11·08	10·12	9·43
		Loss	·31	1·27	1·96 (= 17·2%)
27	90%	11·43	10·9	10·59	9·79
		Loss	·53	·83	1·64 (= 14·4%)

Table V.—*Loss in Weight of Larvae Kept in an Unheated Outhouse, at* 70 *per cent. R.H., Weighed Individually.*

Number of larvae.		1944.			1945.				
		x.	xi.	xii.	i.	ii.	iii.	iv.	v.
16	Average wt. mg.	12·9	11·4	11·1	10·4	10·1	9·8	8·4	8·0
	% of original wt.	100	88·4	86·0	80·6	78·3	75·9	65·1	62·0
30	Average wt. mg.	13·3	—	—	—	—	—	—	8·2
	% of original wt.	100	—	—	—	—	—	—	61·7

4. THE RELATIONSHIP BETWEEN THE ORIGINAL LARVAL WEIGHTS AND THE LENGTH OF THE PERIOD OF QUIESCENCE.

It was found that the heavier larvae have a longer period of quiescence than the lighter ones, irrespective of whether they are kept at outdoor temperatures or are transferred to 25° C., 70 per cent. R.H. This data is summarized in Table VI and in Richards and Waloff (1946).

As diapause is not immediately broken when the early diapausing larvae are placed at the temperature of 25° C., 70 per cent. R.H., it would seem that a certain loss in weight, accompanied by elimination of waste products is necessary before the critical stage is reached. It may be noted that roughly 35 per cent. loss of the original weight occurs before the onset of pupation.

It was also found that the majority of larvae weighing less than 8 mg. die out throughout the winter period (Richards and Waloff, 1946), and the lower weight loss of 27·9 per cent. of the lighter larvae, may be associated with this critical stage.

TABLE VI.—*Pupation Rates of Larvae Quiescent at Outdoor Temperatures and Subjected to 25° C., 70 per cent. R.H., at Different Times of the Year.*

Date placed at 25° C., 70% R.H.	Number of larvae.	Number of pupae.	Per cent. of mortality at 25° C.	Per cent. in diapause.	Number of days at 25° C. before pupation.		Average wt. (in mg.) of larvae pupating on	
					Range.	Average.	1st 10–20 days.	Last 10 days.
19.ix.45	93	55	38·7	52·7	20–290	110	9·2	15·0
18.x.45	94	48	47·9	52·8	20–260	109	7·0	11·5
1.xi.45	93	71	24·5	33·8	20–240	73	9·4	13·5
15.xi.45	93	73	21·5	30·1	20–230	62	7·2	11·0
4.xii.45	93	74	20·4	20·3	10–180	36	8·0	9·5
15.xii.45	84	65	26·4	15·4	20–70	30	7·3	12·5
3.i.46	98	54	44·9	1·8	10–50	20	6·8	12·5
16.i.46	93	84	9·7	3·6	10–60	23	8·5	13·0
2.ii.46	95	81	14·7	0	10–40	16	6·7	11·0
16.ii.46	97	83	14·4	0	10–40	15	7·1	9·0

5. THE EFFECT OF SUBJECTING LARVAE QUIESCENT AT OUTDOOR TEMPERATURES TO 25° C., 70 PER CENT. R.H.

On examining Table VI it will be seen that the period preceding pupation at 25° C., 70 per cent. R.H., is more extended in the larvae placed at this temperature at their wandering period (19.ix.45) and in the weeks immediately following it, than in those placed at high temperature in early January and in the subsequent weeks. Larvae placed at 25° C., 70 per cent. R.H., in early and in the middle of February all pupated within 40 days (16 and 15 days on the average). This period of 40 days was, somewhat arbitrarily, chosen to delimit the non-diapausing from the diapausing larvae. It is clear that by January the larvae at outdoor temperatures (given in Table VIII) reach a certain physiological state in which pupation is delayed not by the original diapause-inducing factors, but by the low outdoor temperatures which delay immediate pupation. The data summarized in Table VII show that the weight loss before pupation is not a constant, but bears relation to the original weight, i.e. roughly there is some 35 per cent. loss of live weight. It has already been suggested that this loss is mainly due to the continuous excretion

TABLE VII.—*Per cent. Weight Loss of Quiescent Larvae Kept at Outdoor Temperatures Between October and May.*

Number of quiescent larvae.	Average weight mg. in October.	Before pupation. April–May.	Per cent. loss of weight.
4	11·1	8·0	27·9
16	12·9	8·0	38·0
30	13·3	8·2	38·2
9	15·6	9·7	37·8
10	15·9	11·2	33·7
7	18·3	12·3	32·8
8	20·4	13·1	35·8
5	24·5	16·3	33·5

throughout quiescence. The process of the release of the pupation hormone in *E. elutella* (Waloff, 1948) does not appear to differ from that in *E. kühniella*, described by Kühn and Piepho (1936). The timing of this can be correlated with the loosening of the hypodermis and the withdrawal of the ocellar pigment. It may be suggested that in *E. elutella* the production of the hormone is delayed until a certain weight loss, accompanied by excretion has occurred.

TABLE VIII.—*Average Temperatures at which the Larvae were kept before Treatment Outlined in Tables VI and IX.*

Date.	Average temperature.	Maximum.	Minimum.
19–30.ix.45	13·2° C.	14·5° C.	7·0° C.
1–28.x.45	15·9° C.	12·6° C.	5·8° C.
29.x–11.xi.45	10·3° C.	12·6° C.	5·4° C.
12–25.xi.45	9·8° C.	11·4° C.	5·0° C.
26.xi–9.xii.45	4·8° C.	10·0° C.	1.1° C.
10–21.xii.45	5·8° C.	10·0° C.	2·2° C.
22.xii.45–4.i.46	4·4° C.	8·9° C.	0° C.
5–20.i.46	3·5° C.	10·6° C.	—1·1° C.
21.i–3.ii.46	5·3° C.	14·4° C.	0° C.
4–17.ii.46	8·9° C.	19·4° C.	5·6° C.

There is no evidence as yet from this work that a diapause-inducing hormone is also produced, but should such a substance exist, it would suggest a possible explanation for the prolonged diapause of the larvae subjected to 25° C. in the early weeks of quiescence; namely, that the high temperature, which increases the general metabolic rate, may also increase the output of the diapause-inducing factor at the critical time of its production.

The possible relationship between the original weights, the length of diapause, and the time of pupation, and the effect of rise of temperature can be summarized in the following diagram (see fig. 1):

In fig. 1 $a>b>c$ and a, b, c, are the original weights of the diapausing larvae. a', b', c', a^{n}, b^{n}, c^{n}, are the maximum and the minimum weights at which pupation occurs. Evidence that $a'>b'>c'$ is set out in Table VII. The period in which high temperature is not effective in initiating pupation is longer in heavy than in light larvae, i.e. $A'>B'>C'$, as this is true of larvae placed at 25° C. at the beginning of diapause (*see* Table VI, and Richards and Waloff, 1946). After a certain critical stage is reached, high temperature initiates pupation, and the period preceding it again bears relation to the larval weight.

6. THE EFFECT OF SUBJECTING DIAPAUSING LARVAE TO —2° C., 55 PER CENT. R.H.

The data in Table IX summarizes the rates of pupation, and the percentages of diapausing larvae in the three sets placed at 25° C., 70 per cent. R.H.

(*a*) Are groups each of 100 wild larvae, kept in an unheated outhouse and then weighed and transferred to 25° C., 70 per cent. R.H., at different times of the year. These are the larvae which have been discussed in Section 5.

(*b*) Are groups of 50 larvae, kept in an unheated outhouse, subjected to — 2° C., 55 per cent. R.H., for periods of about a fortnight (12–19 days) at different times of the year, then weighed and placed at 25° C., 70 per cent. R.H.

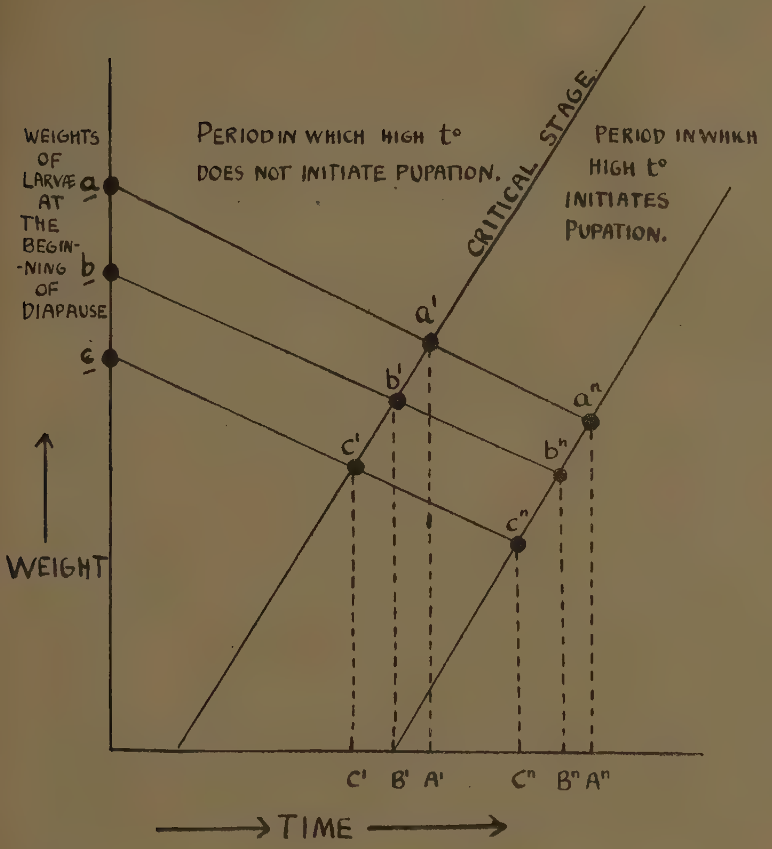
WEIGHTS OF LARVÆ AT THE BEGINNING OF DIAPAUSE
a
b
c
WEIGHT
PERIOD IN WHICH HIGH t° DOES NOT INITIATE PUPATION.
CRITICAL STAGE
PERIOD IN WHICH HIGH t° INITIATES PUPATION.
a'
b'
c'
a''
b''
c''
C' B' A' C'' B'' A''
TIME

Fig. 1.—Diagram to illustrate the relationship between weight and the length of diapause in *E. elutella* larvae.

(*c*) Are groups of 50 larvae all subjected to — 2° C., 55 per cent. R.H., on the same date (23.x.45) and then removed from it at different intervals of time, i.e. after 7, 21, 40, 51, 67, 82 days. The survivors were weighed and placed at 25° C., 70 per cent. R.H.

The average temperatures experienced by the larvae before they were placed at 25° C. or — 2° C. are given in Table VIII.

TABLE IX.—*The Effect on the Rate of Pupation of Subjecting Diapausing Larvae to —2° C., 55 per cent. R.H.*

Date placed at 25° C., 70% R.H.	Number of Days at — 2°C., 55% R.H., before this date.	Per cent. survival at — 2° C.	Average weight on date at 25° C. (mg.)	Number of pupae.	Per cent. imperfect pupae.	Average period to pupation at 25° C., in days.	Per ce in diapau
a. 1.xi.45	0	—	9·9	71	8·2	72·8	33·
b. —	—	—	—	—	—	—	—
c. 1.xi.45	7	100	8·6	28	32·1	68·7	42·
a. 15.xi.45	0	—	9·1	73	8·1	61·5	30·
b. 14.xi.45	14	88	8·6	29	24·1	57·1	34·
c. 14.xi.45	21	100	8·9	39	30·8	74·5	48·
a. 4.xii.45	0	—	8·9	74	7·7	35·9	20·
b. 4.xii.45	19	90	8·2	29	24·1	29·9	10·
c. 4.xii.45	40	100	9·7	25	32·0	50·0	31·
a. 15.xii.45	0	—	8·4	65	7·4	29·8	15·
b. 15.xii.45	12	100	8·7	41	9·8	25	9·
c. 15.xii.45	51	0	—	—	—	—	—
a. 3.i.46	0	—	8·1	54	14·3	19·5	1·
b. 31.xii.45	16	100	7·8	46	8·7	24·2	2·
c. 31.xii.45	67	0	—	—	—	—	—
a. 16.i.46	0	—	8·1	84	3·2	22·8	3·
b. 15.i.46	15	100	6·6	36	21·2	29	13·
c. 15.i.46	82	0	—	—	—	—	—
a. 16.ii.46	0	—	7·5	83	8·4	15·0	(
b. 16.ii.46	15	100	7·6	19	31·6	17·6	(

The significance of the data summarized in Table IX is by no means clear, as it is difficult to separate the time effect from the direct effect of low temperature and of variations in temperature. The following points, however, emerge from these results:

(1) Prolonged continuous exposure to — 2° C., 55 per cent. R.H., kills all the larvae. Whereas they all survived this temperature for 40 days, they were all killed after 51 days and over. This lethal effect of low temperature became apparent after continuous exposures for 21 and 40 days, as the subsequent period preceding pupation at 25° C. was protracted and the percentage of larvae which entered diapause exceeded that of the larvae which had not experienced this low temperature.

(2) Exposure to — 2° C. for a period of about a fortnight in the second half of November, and in early December, appears to have a slight accelerating effect on the subsequent rate of pupation at 25° C. After these dates, similar exposures to — 2° C. have a slight delaying action. After December only a very low proportion of the larvae will diapause, when they are placed at 25° C. directly from outdoor temperatures. It may be suggested that the diapause-inducing factors are eliminated throughout December and that the variations of temperature (i.e. transferring larvae from outdoor temperatures to 2° C. and then to 25° C.), at this critical period, affect the rate of disappearance of these factors.

(3) Exposing larvae to — 2° C. for periods of a fortnight after December have a slight delaying action on the rate of pupation.

(4) There was a considerably higher proportion of imperfect pupations amongst the larvae which had been exposed to — 2° C. than amongst those placed at 25° C. directly from outdoor temperatures. In all cases of imperfect pupation the pupal skin was formed under the larval one, but the larvae failed to moult. It would seem as if exposure to this low temperature upsets the balance of the rates of processes preceding pupation.

7. A BIVOLTINE STRAIN OF *E. elutella*.

There are two generations a year of *E. elutella* in this country. In other countries there may be more. Reed and Livingstone (1937) record three generations on tobacco at Richmond, Virginia, and Ustinov (1932) speaks of three possible generations in Abkhasia. The occurrence of a possible bivoltine stock has already been discussed (Richards and Waloff, 1946).

It was seen that the second generation of moths were derived almost entirely from eggs laid at the beginning of emergence by early moths. Also, the earlier collected larvae produced earlier moths in the following year. These differences may be genetic, but as early larvae are known to be heavier and the weight of fully fed larvae is related to diapause, the effects of crowding and nutritional factors may also be involved.

It appears that, whereas nearly all the larvae have a diapause, there are a few non-diapausing larvae which produce the second generation of moths developing from the eggs laid by the earliest emerging moths of the first generation. Such moths may belong to a genetic stock, part of the offspring of which form the second generation each year. In this connection it is interesting to note that during the population study of this species (Richards and Waloff, 1946) there was a small distinct early emergence of moths, which died out before the beginning of the main general emergence in two successive years —1944 and 1945.

8. A MULTIVOLTINE STRAIN OF *E. elutella*.

A non-diapausing stock, with successive generations, bred on middlings or on Manitoba wheat at 24–25° C., 70 per cent. R.H., has been isolated by Mr. E. B. Basden in the Slough insectaries.

This stock readily re-enters diapause when the conditions of temperature and nutrition are altered. Table X shows the effect of temperature on this stock.

The results set out are somewhat anomalous, as 59 out of 64 larvae, i.e. 92·1 per cent., entered diapause at 21° C. and 19 out of 44, i.e. 43·2 per cent. at 17° C. Nevertheless, they show that the lowering of temperature by only 3° C. is effective in upsetting the balance in the multivoltine stock.

The effect of rearing larvae on different foods also became obvious. It was possible to subdivide the natural foods into three groups : (*a*) Those on which no larvae diapaused at 25° C. 70 per cent R.H. ; (*b*) those on which a low percentage of larvae diapaused at 25° C., 70 per cent. R. H. ; and (*c*) those on which all or a high percentage of larvae diapaused at 25° C., 70 per cent. R.H. The last group was characterised by a high starch content (Waloff, 1948).

TABLE X.—*Development of* E. elutella *larvae on Manitoba Wheat No.* 1.

Temperature.	Survival.	Per cent. in diapause.	Average length of larval life (days).			
			Before spinning up.	Spun up.	Total days.	
					Non-diapausing larvae.	Diapausing larvae.
25° C., 70% R.H.	65/75 = 86·6%	0	—	—	35·9 (limits 29–50)	—
21° C., 70% R.H.	64/75 = 85·3%	92·1	65	196·5	64 (limits 50–80)	249·4 (limits 100–375)
17° C., 70% R.H.	44/75 60%	43·2	66·9	192·6	61·2 (limits 54–80)	272·2 (limits 153–379)

It is not suggested that starch is the primary factor in inducing diapause, but rather that some essential factor was lacking, and that the abundance of starch as such, was impeding development. The inability of this species to utilize starch, its requirements of linoleic acid and a certain percentage of glucose and vitamins of the B complex have been discussed by Fraenkel and Blewett (1943, 1946*a*, 1946*b*), and it may be that some or all of these factors are necessary for the production of the pupation hormone.

Eggs produced by wild moths developed into diapausing larvae, even when reared on Manitoba wheat at 25° C., 70 per cent. R.H. This suggests that genetic factors are responsible for the absence of diapause in the laboratory stock, especially as it has been selected for a period of four years by rejection of the larvae which did not pupate readily. There is, however, a very delicate balance between the nutritional requirements, conditions of temperature and the maintenance of the state of non-diapause in the multivoltine larvae, and the limits within which this state persists are narrow.

9. DISCUSSION.

Ephestia elutella is cosmopolitan in its distribution (Richards and Thomson, 1932), but the readiness with which this species enters diapause suggests that it is an insect of temperate climate. No definite diapause is known to exist in *E. kühniella*, the Mediterranean flour moth, and although this species exists only in very low numbers in unheated conditions, its pupae have been found throughout the winter months (Richards and Waloff, 1947). The non-diapausing stock of *E. elutella* isolated in the Slough laboratories persists at the temperature of 24–25° C., 70 per cent. R.H. The lowering of temperature to 21° C., 70 per cent. R.H., i.e. by only three degrees, again induces diapause. Diapause can also be brought about at 25° C., 70 per cent. R.H., by unfavourable nutritional factors, such as a high starch content in the larval diet. Diapause in the larvae of *Loxostege sticticalis* is said to be associated with unsatisfactory nutrition and low temperature during development (Steinberg and Kamensky, 1936) and that of the braconid parasite (*Chelonus annulipes*) of the

European corn-borer (*Pyrausta nubilalis*) is affected by the host physiology, so that the parasite conforms to the seasonal cycle of the host (Bradley and Arbuthnot, 1938). Moulting in the 4th or 5th instar in *Rhodnius prolixus* is greatly delayed in sterile cultures free from the symbiotic *Actinomyces rhodnii* (Brecher and Wigglesworth, 1944), and the authors put forward a suggestion that growth ceases through some vitamin deficiency, and that possibly the vitamin is needed for the production of the moulting hormone. It is also possible that the production of the pupation hormone is delayed in *E. elutella* by unfavourable nutrition.

Field observations on *E. elutella* have indicated that there probably exists a genetic strain which produces the second generation each year. The earliest laid eggs produce not only the earliest moths of the following year, but also the second generation of the same year. Prebble (1941) quotes several examples of diapausing and non-diapausing genetic strains of the same species. He describes " lines " of European spruce sawfly, *Gilpinia polytoma*, with respect to the inherent tendency towards diapause or continued emergence. Arbuthnot (1944) suggests that there are two distinct biological strains in the European corn-borer in the United States. The possibility of the introduction of different strains of *E. elutella* into the warehouses of this country cannot be dismissed.

In *E. elutella* there is a direct relationship between the initial larval weight and the length of period of quiescence of the fully fed larvae, irrespective of whether they are kept at outdoor temperatures, or at 25° C., 70 per cent. R.H. Throughout quiescence there is continuous elimination of waste products and loss of weight (roughly 35 per cent. of the original) up to the time of pupation. The criterion used to see whether the larvae were in diapause, was placing them at 25° C., 70 per cent. R.H., and noting the time of pupation. Larvae introduced to these conditions immediately after their wandering period, i.e. in September and October, pupated only gradually. Those placed at 25° C. later in the year pupated within a fortnight. It is possible that the introduction of the larvae to high temperatures at the beginning of quiescence increases the output of diapause-inducing factors, and that low outdoor temperatures are needed for the gradual elimination of these. The time of release of pupation hormone in *E. elutella* is, as in *E. kühniella* (Kühn and Piepho, 1936), in the prepupal stage, and it is suggested that its production is delayed until a certain weight loss has occurred. When Prebble (1941) determined the changes in weight of the diapausing *Gilpinia polytoma* pupae, he found that the loss of dry weight was only 2 per cent. during the year, i.e. weight changes in diapause were only slight. Mellanby (1938) found that the diapausing prepupae of *Lucilia sericata* usually contain a higher proportion of dry matter than do the normal individuals. He also found that the smaller individuals either pupate or expire. This is also true of *E. elutella* larvae. Pepper (1944) found no connection between the condition of diapause and that of the biochemical nature of fatty material in *Loxostege sticticalis*, while Busnel and Drilhon (1937) describe the loss in fat content of *Leptinotarsa decemlineata* in hibernation. Andrewartha (1943), who has investigated the effect of low temperatures on the diapause of *Austroicetes cruciata*, puts forward an interesting suggestion that low temperatures affect the stored fat directly and bring about changes which make it available to the animal.

Finally, it may be said that the quiescent stage in *E. elutella* is a complex process, which may be subdivided into three: (*a*) The period of diapause in which high temperature does not initiate pupation, probably coinciding with the time of production of diapause-inducing factors. The nature of these factors is a matter of speculation, and will remain so, possibly until further experiments comprising cross-injections of diapausing and non-diapausing larvae are carried out. It is, however, interesting to note that a loss of 35 per cent. of the original body weight occurs before the larvae will pupate at outdoor temperatures, and that this loss is mostly due to excretion of nitrogenous waste in solution, and simultaneous diminution of the fat body. It suggests that the state of diapause is related to the physiological state of the fat body. (*b*) Period of quiescence, in which pupation is initiated by high temperatures, and is delayed by low outdoor temperatures. (*c*) The prepupal stage, characterized by the more abundant excretion, final emptying of the gut, retraction of ocellar pigment, release of pupation hormone, the final moult and pupation.

10. SUMMARY.

(1) Most of the larvae of *E. elutella* undergo a prolonged period of diapause, which lasts 8–9 months.

(2) As well as this univoltine strain, there exists a bivoltine strain, which produces the second generation each year. A multi-voltine strain has been isolated in the Slough insectaries. The temperature and nutritional limits within which this strain persists are narrow.

(3) The quiescent larvae metabolize slowly, producing solutions of nitrogenous waste continuously. Elimination of this waste is accompanied by loss in weight.

(4) It is suggested that the production of the pupation hormone is delayed until a certain weight loss has occurred (roughly 35 per cent. of the original weight).

(5) The period of quiescence can be subdivided into three—

(*a*) true diapause, in which high temperature does not initiate pupation.

(*b*) quiescence, in which pupation is delayed by low outdoor temperatures and during which high temperature initiates pupation.

(*c*) prepupal stage, characterized by the release of the pupation hormone.

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CONTENTS

PAGE

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   E. B. Ford, M.A., D.Sc., F.R.S., appointed 1949.
2. **Local Committee of Management of Wicken Fen.**
   H. M. Edelsten, O.B.E. (nominated by Committee for the Protection of British Insects).
3. **National Trust for Places of Historic Interest or Natural Beauty.**
   H. M. Edelsten, O.B.E., appointed 1944.
4. **New Forest Association.**
   C. W. Mackworth-Praed, appointed 1948.
5. **New Forest Joint Committee.**
   Lt.-Col. F. C. Fraser, I.M.S., appointed 1949.
   F. J. Killington, D.Sc., A.L.S., appointed 1939.
6. **Royal Meteorological Society. Phenological Committee.**
   C. B. Williams, M.A., D.Sc., appointed 1937.
7. **Council for the Promotion of Field Studies.**
   W. H. Thorpe, M.A., Sc.D., appointed 1944.
8. **Joint Bioclimatic Committee.**
   B. P. Uvarov, C.M.G., D.Sc., appointed 1945.
   C. B. Williams, M.A., D.Sc., appointed 1945.
9. **Yorkshire Naturalists' Trust, Ltd.**
   W. D. Hincks, M.P.S., appointed 1946.

NOTES ON SOME EPHEMEROPTERA BAËTIDAE FROM INDIA AND SOUTH-EAST ASIA.

By M. T. Gillies, B.A., M.B., B.Ch.

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This paper is an account of material collected during the course of military service in India, Siam and Malaya from 1945–1947. Only the family Baëtidae is considered here, but it is hoped to work out the rest of the material at some future date. It must be emphasized that this is not a comprehensive review of the natural history of the species concerned. Much of the work was done under active service conditions. Moves were frequent, the duration of stay in each locality was short, opportunities for collection restricted and materials inadequate. No area was revisited at a later date, so it was difficult to obtain a clear picture of periods of emergence in the different seasons. Most of the collecting was done in a number of areas in India and in a small part of South Malaya. The Indian fauna was found to be much more abundant and varied, but it is likely that the more mountainous regions of Central Malaya may show as great a variety of species as Ulmer has described from Java and Sumatra.

Certain elementary observations on the habits of tropical forms can be made here. Stagnant water forms, such as *Cloëon*, are mostly nocturnal in appearance and emerge the whole year round. They predominate in a constantly hot climate such as Malaya, where even fast-running streams contain nymphs of few other species. In the mountain streams of Northern India there is an abundant hatch in the autumn, and it may be that this continues throughout the spring and summer as well. In the larger rivers of Central India, such as the Narbada and Sonar, adults were found in small numbers during the dry season, but on the Mutha, in Bombay Presidency, they were found in much larger numbers towards the end of the monsoon. Careful search of the neighbourhood of the Sohan in the North-West Punjab during one week in May produced very few of either adults or nymphs, suggesting that here at least the main hatch had been earlier in the dry season. Hatches of duns appear to be infrequent or nocturnal, and so not observed. They were seen on two occasions only, on the Sonar in March, where a mixed hatch of Baëtidae and Leptophlebiidae occurred at dusk, and on a mountain stream in North Bengal in September, also at dusk. Clouds of "dancing" spinners, so familiar in England, were very rarely seen, apart from the winter broods of *Cloëon*. The underside of vegetation along river banks was, however, a much more profitable source of specimens and it was felt that this, together with the associated cobwebs, gave a fair picture of the fly life that had emerged during the previous twenty-four hours.

Much of the previous work on Oriental Ephemeroptera has dealt with the larger and more primitive families, e.g. PALINGENIIDAE, POLYMITARCIDAE, EPHEMERIDAE and POTOMANTHIDAE. Little has been written about the BAËTIDAE. Ulmer, however, in a very detailed and comprehensive work (1939) has covered the whole known fauna of the Netherlands East Indies, and Kimmins (1947) has recently reviewed critically the Indian species of *Cloëon*. Traver (1939) has also described some BAËTIDAE amongst a collection from Kashmir. Notes are given here on five genera and twenty species, all of this family, of which five have been previously described and eleven are new. The types of all new species have been presented to the British Museum (Natural History), and the descriptions all apply to specimens in 2 per cent. formaldehyde unless stated to the contrary.

I must record here the great assistance that I have received from Mr. D. E. Kimmins, of the British Museum, and the free use of files and references that he has very kindly permitted. I should also like to express my thanks to Dr. T. T. Macan, of the Freshwater Biological Association, for much useful advice and criticism and for communicating this paper, to Dr. B. N. Chopra, late Director of the Zoological Survey of India, and to Mr. M. W. F. Tweedie, of the Raffles Museum, Singapore. I am also indebted to the Secretary of the Bombay Natural History Society for the storage of specimens after I left India.

Baëtis Leach.

No species of *Baëtis* or *Acentrella* have up to now been described from India. Eaton (1885) mentions in a few lines an undescribed female from "Hindostan." From Ceylon, Hagen (1858) described *B. consuetus* and *B. solidus*, and Eaton, after his account of these two, adds *B. feminalis*. He gives, unfortunately, no figures of these species. *B. feminalis* may, indeed, not have been a *Baëtis* at all, as he remarks on the absence of hind wings in all available specimens. From Java and Sumatra, Ulmer, in 1913, described *B. javanica* and later (1939) *B. sumatrana*, *B. olivascens* and *Acentrella fulmeki*.

An account is given here of eight species from India and one from Malaya, of which six are described and figured as new species. The remainder are only known as females and it was not considered justifiable to describe them. They were collected mostly in two widely separated areas in India, namely, the foot-hills of North Bengal and the River Mutha, near Poona, both very different habitats.

They are similar in general to European species, although the Malayan specimen is noteworthy for the remarkably small size of the hind wing, smaller than in most species of *Centroptilum* yet typical of *Baëtis* in shape. Two species, *B. dipsicus* and *B. palmyrae*, belong to the *Acentrella* group. I have here placed them all in *Baëtis*, as the exact relationship of *Acentrella* to *Baëtis* is still in doubt. These two differ from the others only in lacking a costal spur in the hind wing and, in *palmyrae*, by the hind wing being smaller than usual and very slightly smaller in the female than in the male.

Towards the end of the monsoon appears to be a favourable time in India for their emergence. *B. fluitans* was particularly abundant in the rain-swollen waters of the River Mutha (air temperature 70–85° F. in September) together with fewer numbers of *B. palmyrae* and *B. dipsicus*. On the other hand, a single specimen of *B. palmyrae* was caught on the Narbada in the hot dry weather of April. In the cooler waters of the Himalayan foothills (*c.* 70° F., air 65–78° F. in September at 4000 ft.) their period of main emergence is probably a little sooner than in the plains. Few nymphs were found then, although those of other genera, e.g. *Epeorus*, were abundant.

A table is set out below giving some of the principal characteristics of the new species and those of other authors :

Principal characteristics of species of Baëtis.

Species.	Body (mm.).		Wing.		Turb. eyes.	H.W. veins.	Tergites 2–6.	Tails.	Stigma veins.
	♂.	♀.	♂.	♀.					
solidus Hag.[1]	4	–	4½–5	–	.	2	Yellow-brown	White	3–6 comp.
consuetus Hag.[1]	3–4	4½	4½–5	5–6	.	3	Reddish brown	Sepia grey	2–5 simple
feminalis Etn.[1], [4]	4½	4½	5½	6	.	–	Reddish brown	Sepia brown	2–5 simple
javanica Ulm.[2]	9	10	9	11	Brown grey	2	White and red	Grey brown	14–20
sumatrana Ulm.[2]	5	5	5	5	Hazel	2	White	Grey	4 simple
olivascens Ulm.[2], [5]	4–5	4–5	4–4½	4–4½	Umber	2	Olive brown	–	4–5 comp.
fulmeki Ulm.[2], [6]	5	5	5	5	Yellow-brown	2	White	Light umber	8–9 simple
dipsicus sp. n.[3], [6]	6	7	6–6½	8	Blue-grey	2	Yellow-green	White	6–10 simple
palmyrae sp. n.[3], [6]	4	4	4–4½	4–4½	Buff	2	White	White	4–7 simple
fluitans sp. n.[3]	3½	3½	3½–4	3½–4	Dark red	2	White	White	5–6 comp.
tigroides sp. n.[3], [7]	6½	6½–7	6½	7½–8	Reddish yellow	3	Red and yellow	Dark brown	7–9 simple
thurbonis sp. n.[3]	6	.	6	.	Dark red	3	Lemon	White	3–6 comp.
solitarius sp. n.[3]	4½	.	4½–5	.	Brick red	2	Lemon	White	6–7 comp.

[1] Dried specimens. [2] In spirit. [3] In life. [4] Femora banded. [5] C, Sc area olive brown. [6] *Acentrella* group. [7] Sooty wing-tip and root.

Baëtis dipsicus sp. n. (figs. 1, 10 ; forceps, hind wing).

Male imago (in life).—Eyes pale bluey grey. Thorax buff. Abdomen yellowish green, olive green at posterior margins of segments ; tergites 8–10 buff. Forceps and tails white. All femora sandy brown with a ginger spot at the apex ; tibiae and tarsi translucent white.

(In fluid).—Head orange brown ; turbinate eyes separated apically, brownish red in colour, yellow round the sides ; lower portion black, ocelli white ; first two antennal segments yellowish cream, umber at the joint, remaining segments colourless. Thorax generally orange brown, sternites rather darker. Abdomen : Tergites 2–6 semi-opaque white, shading off to faint brownish laterally ; posterior margins dark brown, this margin broadening on the flanks and being most distinct on segments 2 and 3 ; tergites 7–10 opaque brownish cream, 8 rather darker ; sternites 1–6 cream, 7–10 orange cream. Genital forceps (fig. 1) white ; basal joint as long as second, which tapers evenly distally and has a small rounded tubercle on the inner side near the base ; third joint twice as long as second, broader in the distal two thirds ; fourth joint very small, globular and incompletely divided from the third joint. Tails white. Legs : Fore femur yellowish orange, tibia and tarsus white except for the last two tarsal joints and claws, which are dusky; other femora yellowish, tibiae and tarsi white. Proportions of fore leg, femur : tibia : tarsus, 22 : 34 : 35; tarsal joints, 1 : 10 : 6 : 4 : 3. Wings translucent colourless, veins very pale yellow; stigmatic area contains 6–10 simple or very occasionally forked, slanting veinlets; hind wing 0·8 × 0·2 mm., small, narrow, with rounded end and complete absence of costal spur (fig. 10).

Female imago (in life).—Thorax and abdomen deep ginger brown, metanotum darker. Proximal half of tails grey, distal half white. Femora ginger, tibiae sandy brown.

(In fluid).—Head mauve; oculi blackish mauve, ocelli grey; antennae grey. Thorax: Pronotum buff; mesonotum the same but darker round the margins and with a very distinct pitch brown median line; metanotum darker and more of a chocolate brown; pleurites orange brown; sternites orange, except in the inter-coxal area of the mesothorax, which is cream. Abdomen, when void of eggs, translucent white tinged with pink; when full, deep orange brown; posterior and lateral margins of tergites 1–9 tinged with pink, most marked in segment 1; by reflected light there appears on tergites 6–9, on either side of the mid line, a light brown line extending from the posterior margins two-thirds of the way to the anterior margin and interrupted at its middle; tergite 10 orange; sternites pinkish cream. Tails white. Wings as in male, except that the veins are rather darker, especially at the wing root. Legs: All femora orange; tibiae and tarsi white, except for last tarsal joints and claws, which are dusky.

Body-length: Male 6 mm., female 7 mm. *Wing*: Male 6–6½ mm., female 8 mm. *Tails*: Male 11 mm.

INDIA: River Mutha, four or five miles above Poona.

The type-specimens, four males and two females, were found on the underside of the fronds of palm trees in the bushes along the bank of the river, on 10 and 11.ix.45.

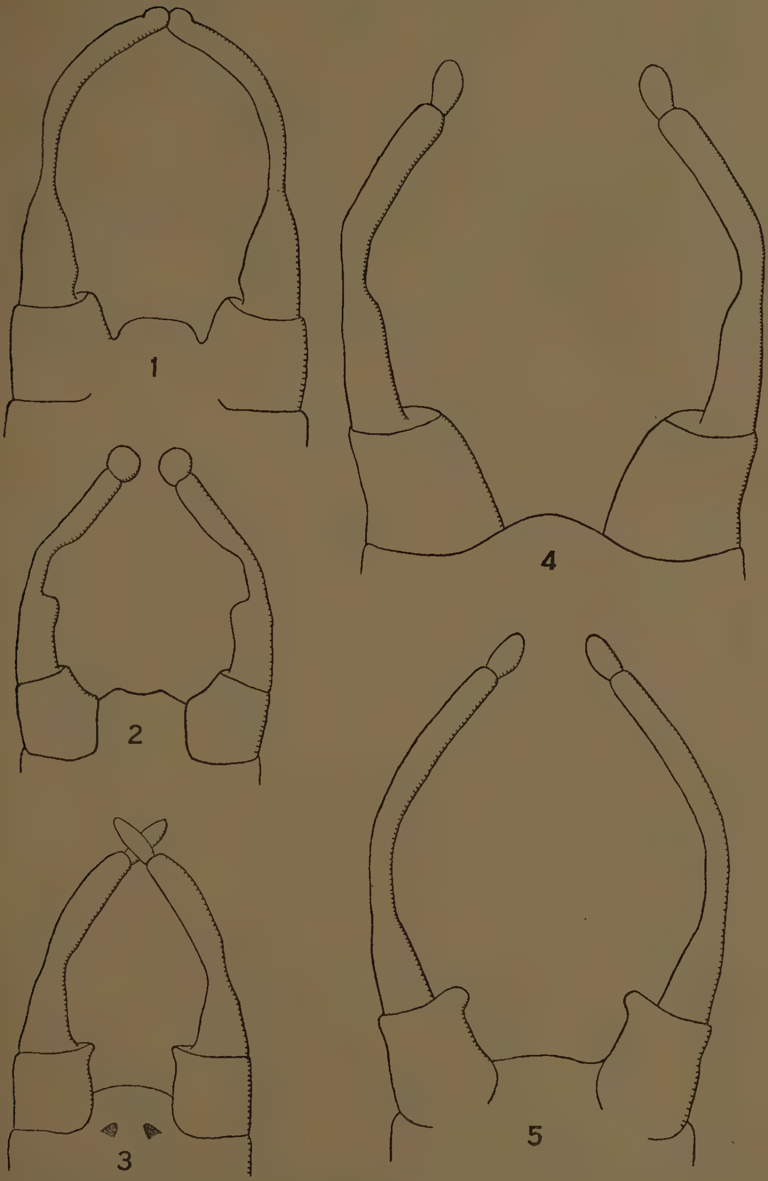
This is a largish species of the *Acentrella* group, readily distinguished by its size, brown and green coloration and characteristic forceps. *A. fulmeki* Ulmer has a similar hind wing, but differs in the shape of the forceps and in coloration, and the eyes are contiguous apically.

Baëtis palmyrae sp. n. (figs. 2, 14, 15, forceps, hind wings).

Male imago (in life).—Eyes light sandy brown. Thorax pitch brown. Abdomen translucent cream; segments 1, 3, 5 and 6 tinged with pink, 7–10 sandy brown. Tails and forceps white. Legs cream except for the fore tibia, which is dusky; femora all bearing a red spot at the distal end.

(In fluid.)—Head: Turbinate eyes orange red, contiguous at their apex and overlapping the pronotum completely, lower portion blackish; ocelli white; basal two antennal segments white, remainder colourless; basal joint has a small spine on the lateral aspect of its distal end. Thorax uniform reddish brown. Abdomen: Tergites 2–6 translucent white, 7–10 opaque cream; sternites as tergites. Forceps (fig. 2) white; basal joint as long as second, directed slightly outwards; second joint untapered and without tubercle; third joint twice as long as second, bent sharply inwards at the end of its proximal one-third and becoming thicker at this point; fourth joint large and globular, and completely separated. Tails white. Legs uniformly white, claws dusky. Proportions of fore leg, femur : tibia : tarsus, 23 : 32 : 25; tarsal joints, 1 : 12 : 8 : 4 : 2. Wings translucent colourless; veins very pale yellow, except round the wing root, where they are reddish brown; stigmatic area contains 4–7 incomplete slanting veinlets; hind wing 0·6 × 0·1 mm., narrow, spurless and with two veins (fig. 14).

Female imago.—Head: Oculi purplish black, ocelli white; basal antennal segment brown, second segment cream. Thorax orange brown. Abdominal tergites semi-translucent brownish pink, brown along the posterior margins; on tergites 2–6 the spiracular



FIGS. 1–5.—Forceps of *Baëtis* species (to scale). (1) *B. dipsicus.* (2) *B. palmyrae.* (3) *B. fluitans.* (4) *B. tigroides.* (5) *B. thurbonis.*

line is marked clearly blackish along the lateral margins; sternites white, tinged with pink, especially in segment 10. Tails missing. Legs: Femora brownish cream, tibiae white, claws dusky. Wings as in male, except that the hind wing is slightly, but distinctly, smaller (fig. 15).

Body-length: Both sexes, 3½–4 mm. *Wing*: 4–4½ mm.

INDIA: River Mutha, four or five miles above Poona. River Narbada, six miles above Hoshangabad, C.P.

The type specimens were four males and two females from the Mutha, taken on 10 and 11.ix.45. The males were found resting underneath the fronds of low palms along the bank of the river, the females spent on the surface of the river. The Narbada specimen was caught alive in a cobweb at midday on 19.iv.45, air temperature 100–108° F.

This is a small species, easily recognized by the very reduced, spurless hind wing and the characteristic forceps with the large globular terminal joint.

Baëtis fluitans sp. n. (figs. 3, 18, forceps, hind wing).

Male imago (in life).—Eyes dark red. Thorax pitch brown. Abdominal segments 2–6 translucent white, 7–10 dark reddish brown. Tails white.

(In fluid.)—Head umber; turbinate eyes dark red, separated apically, lower portion blackish; ocelli white; basal two antennal segments brownish cream, remainder white. Thorax uniform umber, sutures darker. Abdomen: Tergites 2–6 translucent white, 7–10 opaque sandy brown; sternites 2–6 white, 7 and 8 cream, 9 and 10 sandy brown, darker at the margins and round the forceps base; at the junction of the ninth and tenth sternites, between the basal joints of the forceps, are a pair of dark brown spots, slightly elongated laterally and forwards. Forceps (fig. 3): First joint brown, remainder white; first joint subequal to second and with a distinct tubercle on its inner distal lip; second tapering slightly and evenly; third joint one and a half times as long as second, tapered slightly proximally; fourth joint thin, pointed and rather less than half the length of the third joint. Tails white. Legs translucent colourless. Proportions of fore leg, femur : tibia : tarsus, 16 : 25 : 21; tarsal joints, 1 : 8 : 6 : 4 : 2. Wings translucent colourless; subcosta and first radial branch brownish by reflected light, yellowish by transmitted light; other veins tinged with the very faintest yellow; stigmatic area contains 5 or 6 simple, slanting veinlets; hind wing small, 0·6 × 0·25 mm., rounded with an acute spur, two veins and a trace of a third vein (fig. 18).

Female imago (in life).—Thorax and abdomen dark sherry brown, cream on the underside. Tails white. Legs sandy brown.

(In fluid.)—Head orange brown; oculi black, ocelli blackish grey; first two antennal segments reddish brown, remainder pinkish. Thorax orange brown. Abdominal tergites 2–6 semi-translucent pink, posterior margins rather redder; remaining tergites reddish orange; sternites white. Tails white. Legs uniform translucent white, hind claws dusky.

Body-length: Both sexes, 3–3½ mm. *Wing*: 3½–4 mm.

INDIA: River Mutha, four or five miles above Poona.

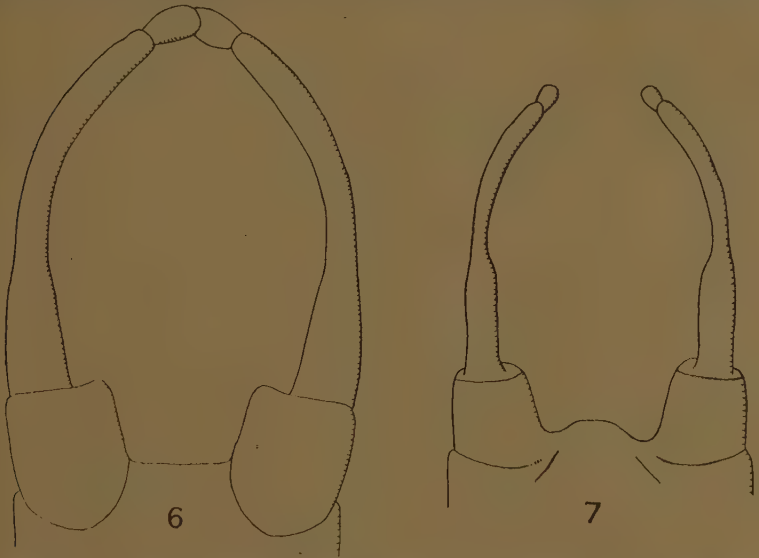
The type specimens, four males and two females, were caught on 10 and 13.ix.45. On the former occasion the females were coming down, floating on the surface of the river, in large numbers all day. Both sexes were also abundant in the bushes and cobwebs along the bank. This species seemed to be much the most common fly at this time of year, when the river is swollen with the rains and weather not too hot.

This is a small species, recognized by the characteristic forceps in the male, lack of pigment in the wings and small rounded hind wings with two veins and a trace of a third. The females are very similar in appearance to *B. palmyrae* and are only distinguishable with certainty by the hind wings.

Baëtis tigroides sp. n. (figs. 4, 8, 9, forceps, wings).

Male imago (in life).—A rather handsome red and yellow fly, striped in parts. Head yellow, eyes brick red, paler at the sides, ocelli black. Thorax pitch brown. Abdomen generally red and yellow, tergites 1–5 yellow with the posterior margins red, 6–9 yellow background with striking red markings, 10 mainly yellow. Tails yellowish red, forceps white. Fore wing bimaculate. Fore legs reddish ginger throughout ; other legs, femora yellow, proximal half of tibia brownish ginger, distal half and tarsi yellow.

(In fluid.)—Head pale orange ; turbinate eyes strikingly tall and cylindrical, only slightly broader at the apex than at the base, reddish orange on top, yellowish round the sides and becoming redder at the base ; lower portion black, ocelli pale grey, each with a black ring round its base ; antennae white throughout. Thorax generally chocolate brown and white ; pronotum white ; tip of mesonotum white, remainder chocolate, except for two irregular white lines that radiate from the posterior end of the median furrow to just in front of, and just behind, the wing root respectively ; metanotum rather paler chocolate ; pleurites and sternites white, except for a narrow chocolate band extending from the wing root to the middle of the anterior border of the mesosternum. Abdomen semi-opaque cream ; tergites 2–5 cream, 6 and 7 pinkish, 8–10 browner ; posterior margins of 2 and 3 dark brownish red, broadening out at the sides ; tergite 9 also has dark brown flanks ; on tergites 4–8 is a paler median line and on either side of this, on segments 6 and 7, is a faint pale, divergent stripe running backwards and slightly laterally, this being most distinct on segment 6, less so on 7 and doubtfully present on remaining segments ; sternites uniform cream. Forceps (fig. 4) white ; basal joint rather longer than broad, equal to



Figs. 6–7.—Forceps of *Baëtis* and *Pseudocloëon*. (6) *B. solitarius*. (7) *P. inopinum*.

second joint, which is thin and with a few distinct hairs on its inner border; third joint long and thin, bent in rather sharply near the base; fourth joint small and ovoid. Legs white; proximal half of hind and mid femora brownish. Proportions of fore leg, femur : tibia : tarsus, 28 : 48 : 40; tarsal joints, 1 : 17 : 12 : 7 : 2½. Wings generally translucent colourless; area round wing root and outer one-quarter of costal and subcostal areas sooty brown (fig. 8); veins strongly formed; main veins round the wing root, C, Sc and R_1 in the pigmented area of the wing tip, all cross veins and occasional portions of the main veins where they are adjacent to the cross veins, sooty brown; stigmatic area contains 7–9 simple, slanting cross veins; marginal intercalaries rather long; hind wing 0·7 × 0·2 mm., spatulate with central spur and three veins (fig. 9).

Female imago (in life).—Eyes and thorax dark brown. Abdomen burnt umber, with indistinct darker markings. Tails deep umber. Legs: Femora ginger with lighter patches, tibiae with proximal half umber, distal half translucent grey.

(In fluid.)—Head dark brown; oculi blackish grey, ocelli paler; basal two antennal segments cream, remainder sooty. Thorax: Notum dark sherry brown, pleurites and sternites cream. Abdominal tergites 1–9 dark sherry brown, shading off to yellowish brown laterally; tergites 4–5 rather paler, 8–9 contain rather more yellow; tergite 10 yellow; sternites 1–7 yellowish cream, 8 and 9 browner; sternites are marked with a distinct single yellow dot on either side of the mid line; posterior margin of segment 7 is slightly broadened over the openings of the two oviducts. Tails uniform dark sherry brown. Legs: Femora yellowish cream; proximal half of tibiae reddish brown, distal half and tarsi sooty, darkest in the fore tarsus. Wings pigmented as in the male, but all veins are sooty brown throughout, including those of the hind wing.

Body length: Male 6½ mm., female 7–7½ mm. *Wing*: Male 6–6½ mm., female 7½–8 mm. *Tails*: Female 19–20 mm.

INDIA: Mountain streams between 4000 ft. and 5000 ft. round Mirik, N. Bengal.

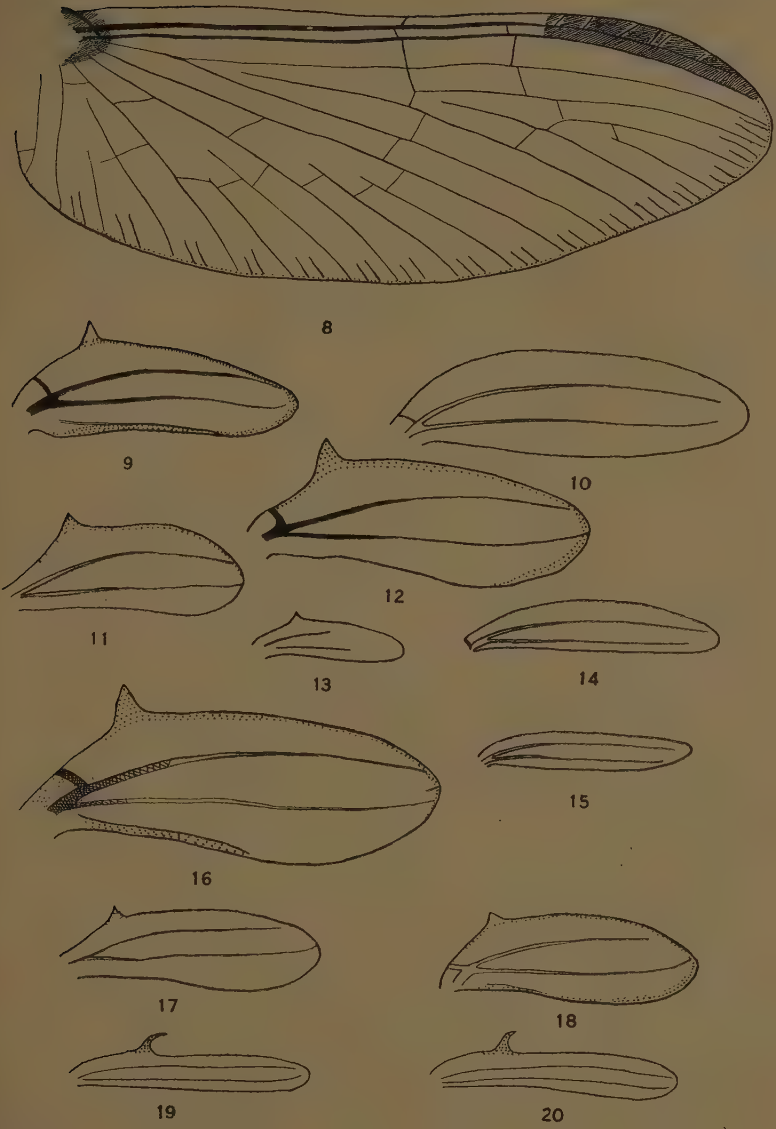
The type specimens, one male and four female imagines, were caught at rest on the underside of foliage overhanging streams between the 18th and 24th September, 1946. Females were seen not infrequently, but only one male was found. One female was observed egg-laying over a small waterfall, bearing a bundle of orange eggs.

This is a large species recognized at once, in both sexes, by the bimaculate pigment in the wings, which readily distinguishes it from all other species.

I also have specimens of two subimagines and one imago, all females, that appear to vary a little from the above description. They differ in that the stigma contains a series of horizontal veinlets in addition to the simple cross veins, the abdominal sternites are marked with a dash on each side as well as a dot and the pigment in the wings is slightly fainter. They have, however, a similar shaped hind wing, characteristic dark venation and long tails. These specimens were seen to emerge at dusk, temperature 67–68° F., from a small, fast-flowing aqueduct. The hatch continued after dark. On first hatching these duns had black eyes, chrome yellow bodies and legs, with ginger margins to the segments and pale grey wings.

Baëtis thurbonis sp. n. (figs. 5, 16, forceps, hind wing).

Male imago (in life).—Eyes dark red; thorax burnt umber. Abdominal tergites 1–6 very pale lemon, posterior margins ringed with dark orange, 7–10 dark orange brown. Tails white, ringed faintly with red. Femora sandy brown, darker at the apex; claws dusky, remainder of legs white.



FIGS. 8–20.—Wings of *Baëtis* and *Centroptilum* species (to scale). (8) *B. tigroides,* fore wing (not to scale). (9) *B. tigroides,* hind wing. (10) *B. dipsicus.* (11) *B. solitarius.* (12) *Baëtis* sp. 1. (13) *Baëtis* sp. 3. (14) *B. palmyrae,* ♂. (15) *B. palmyrae,* ♀. (16) *B. thurbonis.* (17) *Baëtis* sp. 2. (18) *B. fluitans.* (19) *C. campestre.* (20) *Centroptilum* sp.

(In fluid.)—Head : Turbinate eyes not especially large, separated apically, orange red, lower portion purplish black ; ocelli grey with dark basal ring ; antennae reddish brown. Thorax generally pale chocolate brown with pale cream areas on either side of the mesonotum opposite the wing roots and in the mid line posteriorly ; pleurites and sternites buff, metasternum paler ; anterior margins of mesopleurites and mesosternum burnt umber, forming a dark ring from wing root to wing root. Abdominal tergites 2–7 translucent white, 8–10 opaque yellowish cream. Basal forceps joint cream, remainder translucent white (fig. 5) ; first joint rather longer than broad, second narrow and evenly tapered, third long and of uniform thinness, fourth joint slightly elongate. Tails white. Legs white, claws dusky ; fore femur pale brownish cream, darker at the distal end. Proportions of fore leg, femur : tibia : tarsus, 35 : 46 : 36 ; tarsal joints, 1 : 14 : 12 : 6 : 3. Wings translucent colourless, except for a little dark brown pigment round the wing root ; veins pale amber ; stigmatic area very faintly milky, containing 3–6 irregular, slanting cross veins and a broken line of irregular, horizontal veinlets ; hind wing rather large, 1 × 0·4 mm., ovate, with three veins, and a sharp spur (fig. 16).

Body-length : Male 6 mm. *Wing* : Male 6 mm. *Tails* : Male 16–17 mm.

INDIA : Thurbo Tea Estate, Mirik, N. Bengal, alt. 4000 feet.

One male imago was caught at rest under foliage over a mountain stream on 20.ix.46.

This species is best distinguished by the large hind wing with three veins, the dark mesosternal ring in the thorax and the shape of the forceps. *B. consuetus* Eaton would appear to be smaller and to have simple veins in the pterostigma.

Baëtis solitarius sp. n. (figs. 6, 11, forceps, hind wing).

Male imago (in life).—Eyes brick red ; thorax buff ; abdominal segments 2–6 pale lemon yellow, 7–10 buff ; tails white ; femora lemon, rest of legs white.

(In fluid.)—Head reddish brown ; turbinate eyes red, orange round the sides, lower portion black ; ocelli purple ; basal antennal segments reddish brown, remainder colourless. Thorax : Mesonotum dark sherry brown, metanotum paler ; pleurites and sternites cream. Abdominal segments 2–6 translucent white, 7–10 yellowish cream. Forceps (fig. 6) cream ; basal joint slightly longer than broad, second joint narrow and tapered, third long and uniformly slender, fourth joint rounded and slightly elongate. Tails white. Legs generally white, fore femur yellowish. Proportions of fore leg, femur : tibia : tarsus, 20 : 30 : 36 ; tarsal joints, 1 : 17 : 10 : 5 : 3. Wings translucent colourless ; costal and subcostal area appear faintly milky by reflected light ; veins pale amber ; stigmatic area contains 6–7 irregular, branched, horizontal and vertical veinlets ; hind wing 0·5 × 0·2 mm., ovoid with well-formed costal spur and two veins (fig. 11).

Body length : Male 4½ mm. *Wing* : Male 4½–5 mm. *Tails* : Male 13–14 mm.

INDIA : Mirik, N. Bengal, 4000 ft.

One male imago was caught at rest on foliage on 20.ix.46.

This species superficially resembles *B. thurbonis*, but is smaller, lacks the dark mesosternal ring, and the hind wing has only two veins. The relatively long fore tarsus would appear distinctive, unless this is due to malformation. Eaton's description of *B. solidus*, from dried specimens, might possibly apply to this species, although the darker thorax of the latter would probably distinguish it.

Baëtis sp. 1 (fig. 12, hind wing).

Female imago (in life).—A small dark species. Eyes blue. Thorax buff. Abdomen dark sandy brown, posterior margins darker reddish brown, tergites 8–10 still darker.

Tails burnt umber and rather long. Wing venation blackish, stigma contains 4–5 veinlets. Hind wing as in fig. 12.

Several females from Mirik, N. Bengal, 18–23.ix.46.

Baëtis sp. 2 (fig. 17, hind wing).

Female imago (in life).—A small fly. Thorax reddish brown. Abdomen uniform claret red, underbelly cream. Tails white. Stigma contains 7 incomplete, slanting veinlets. Hind wing as in fig. 17.

One female imago was caught at sunset on 23.v.45 on the river Sohan at Chak Lala, near Rawal Pindi.

Baëtis sp. 3 (fig. 13, hind wing).

This specimen, from Malaya, is represented by one fragmentary female and is characterized by the extremely small hind wing, by the single marginal intercalary in the second medial interspace of the fore wing and by the absence of intercalaries behind this.

From a cobweb, 15.i.47, at Kota Tinggi, Johore State.

Pseudocloëon Klapálek.

This genus is widely distributed in India and the Far East. From the Western Ghats Navás has described *P. rubellum* and another species is here added to the Indian list from N. Bengal. *P. kraepelini* Klapálek is also recorded here from Malaya.

Pseudocloëon kraepelini Klapálek.

One male imago, very probably of this species, was caught on overhanging foliage at the waterfall near Kota Tinggi, S. Malaya, on 15.i.47. The fore tarsus is only slightly longer than the femur (*cf.* Ulmer, 1939, tarsus $1\frac{1}{2}$ × femur) but in other respects the specimen agrees well with his description.

Several nymphs were also caught on the sandy bed of this fast-flowing stream, where they seemed to represent the only fauna. These are very similar to Ulmer's *Pseudocloëon* sp. 1, although differing slightly in the shape of the tenth tergite and in the marking on the head.

Pseudocloëon inopinum sp. n. (fig. 7, forceps).

Male imago.—Head : Turbinate eyes very tall, separated apically, reddish orange on top, yellow round the sides ; lower portion black, ocelli grey ; basal two antennal segments brownish mauve, remainder colourless. Thorax : Notum and pleurites buff, sternites cream. Abdominal segments 2–7 translucent white, 7–10 greyish brown, 10 rather lighter ; sternites 7–10 brownish cream. Basal forceps joint (fig. 7) brownish, remainder dusky ; basal joint rather longer than broad, second joint long and narrow, third joint tapered slightly proximally, fourth joint ovoid. Penis cover present. (Tails probably white.) Legs uniform white, fore femur touched with yellow. Proportions of fore leg, femur : tibia : tarsus, 10 : 32 : 21 ; tarsal joints, 1 : 8 : 7 : 3 : 2. Wings translucent colourless ; by reflected light the outer half of C and Sc area is faintly milky ; veins very pale amber ; marginal intercalaries in first cubital interspace paired, in second interspace single and absent behind this ; stigmatic area contains 1–2 incomplete cross veins.

Body length : Male 5 mm. *Wing* : Male $4\frac{1}{2}$ mm.

INDIA : Mirik, N. Bengal, 4000 ft.

Two males were caught at rest on foliage on 20.ix.46.

This species differs from *P. kraepelini* Klapalek and *P. obscurum* Ulmer, in the tall, narrow, turbinate eyes, which are well separated apically, and from *P. boettgeri* Ulmer by the short fore femur and thinner forceps. The nearly related *Baëtiella ladakae* Traver has a shorter fore tarsus (equal to femur) and the terminal joint of the forceps is elongate. *P. rubellum* Navás, apparently described from a female, would appear to be smaller and to have characteristic markings on the notum, as well as on the abdomen.

Centroptilum Eaton.

Only one species of this genus, *C. vitellinum* Ulmer (1939) from Borneo, has been described from the Orient (outside Japan). Two species are here recorded from India, one being described as new.

Centroptilum campestre sp. n. (fig. 19, hind wing).

Male imago (in life).—Eyes red. Thorax light buff. Abdomen greyish buff, shading off to yellowish posteriorly, sternites cream. Tails pure white.

(In fluid.)—Head : Turbinate eyes pale orange, slightly separated apically, lower portion greyish black, ocelli grey ; basal two antennal segments cream, remaining segments colourless. Thorax generally buff, darker at the sutures ; pronotum yellowish. Abdominal tergites 2–6 translucent yellowish orange, whiter along posterior margins, 7–10 opaque pale orange ; sternites yellowish cream, ninth sternite bordered laterally with dark brown. Basal joint of forceps yellowish cream, remaining joints white ; structure much as in *C. pennulatum* Eaton, second joint short, tapering sharply distally, third joint long, tapering markedly proximally, fourth joint small and thin. Tail(s) white. Legs : Fore femur lemon yellow, tibia and tarsus translucent white ; other femora yellowish cream, tibiae and tarsi white. Proportions of fore leg, femur : tibia : tarsus, 17 : 21 : 24 ; tarsal joints, 1 : 10 : 7 : 4 : 2. Wings generally colourless ; C and Sc areas, in the inner two-thirds tinged with the very faintest yellow, in the outer one-third, distinctly clouded pale yellow ; C, Sc and R1 pale yellow, other veins colourless ; stigmatic area contains 6 simple, slanting cross veins ; hind wing very small, narrow, with rounded apex and tall, thin and recurved costal spur (fig. 19).

Body length : Male 5 mm. *Wing* : Male 4–4½ mm.

INDIA : River Sonar, near Saugor, C.P.

One male was captured at dusk as a subimago on the surface of the river, 11.iii.45.

This species is distinguished from *C. vitellinum* Ulmer by the yellow tinting in the wings and the uniform light colouring of the thorax.

Centroptilum sp. (fig. 20, hind wing).

Female imago (in life).—Eyes and thorax emerald green. Abdomen slightly darker green, posterior margin of each segment reddish brown ; ninth sternite emerald green. Tails uniform very pale green. Legs white, femora reddish brown. Wings translucent colourless ; stigma contains 4–5 cross veins ; hind wing as in fig. 20.

Body length : Female 6 mm. *Wing* : Female 6½ mm.

INDIA : Mirik, N. Bengal, 4000 ft.

One female was captured over a mountain stream on 18.ix.46. The dun has dusky wings and a light olive green body.

Cloëon Leach.

This genus is the most commonly encountered by the casual collector in the tropical parts of the East, and it is not surprising that a considerable number of species have been described. Some of these accounts are of males and some of females, and it is not always possible to arrive at a definite conclusion as to the specific differences involved. Lestage (1929) gave a key to the identification of the then known species and also commented on the difficulties of comparing descriptions based on different sexes. Perhaps the idea of using females as holotypes, as suggested by Kimmins (1947), would do much to clarify the position until more certain specific characters for the males can be found. This method has certainly simplified the identification of Indian species.

In a hot, humid country such as Malaya few other genera are met, unless more careful search is made. Their flying time is almost entirely confined to twilight or the night, but in India, and also in Rangoon and Bangkok, males may be seen dancing by day in the winter. The same may be said of the nearly related genus *Procloëon* Bengtsson. *P. harveyi* Kimmins seems to flourish under all climatic conditions, ranging from the intense dry heat of the summer in Central India to the sticky warmth of Malaya or Bengal during monsoon times. *C. bicolor* Kimmins also seems to have a wide climatic as well as geographic range.

Fourteen species of *Cloëon* and two of *Procloëon* have been described from India and South-East Asia, exclusive of four species not known outside China (Ulmer, 1936). Of these, *C. rubellum* Navás (1923) and *C. taeniatum* Navás (1932) are described from males only and are difficult to compare. *C. viridis* Kimmins (1947), *C. virens* Klapálek (1905) and *C. coomani* Navás (1934) would seem to form a closely related group with greenish marginal pigment in the wings. *C. bicolor* Kimmins (1947) and *C. kashmiri* Traver (1939) are distinctive species from India, and *C. marginale* Hagen and *C. bengalense* Kimmins (1947) are mutually similar species, all four with mainly brown marginal areas. *C. fluviatile* Ulmer (1919) from New Guinea, and *C. exiguum* Navás (1918), from the Philippines, both have very faint yellow pigment in the wings. *C. apicatum*[1] Navás (1932) has pigment in the apex of the wings and *C. variegatum* Chopra (1924) and *C. pulchellum* Banks (1913), both from India, have clear wings.

I give notes here on two of these species from India and Malaya and also describe two new clear-winged species from Malaya and Siam and one from India. I follow Kimmins in placing *bimaculatum* and *harveyi* in *Procloëon*, though without adding any new species to the genus. I am indebted to him for very kindly comparing my specimens with his types.

Like the European *C. dipterum* L., several Oriental species are ovoviviparous. Ulmer (1912) has described the phenomenon in *P. bimaculatum*. Dissection of specimens in my collection has shown the presence of one-half to two-thirds grown embryos in *C. bicolor* from Saugor and *P. harveyi* from Bengal.

Cloëon bicolor Kimmins.

This species was described from Bengal. My specimens are from Calcutta, 6.xii.45; Saugor, C.P., 8.iii.45; Budni, Bhopal, 11.iv.45; Bangalore,

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[1] Navás has also given this name to a species from Central China, in which the marginal area is yellowish. (1933, *Notes ent. chin.* **9** : 17).

7.xi.45; Bangkok, 6.i.46; and Singapore, 17.i.47. The Malayan specimen is a little smaller than the rest. Some examples from Bangalore appeared in life to be similar to *C. bengalense* Kimmins, but are now so faded as to be indistinguishable from *bicolor*.

Cloëon viridis Kimmins.

This was also described from Bengal. I have specimens from Jhikargacha, W. Bengal, 4.vii.45; from a ship at the mouth of the Hooghly in October, and from Bangalore, 15.xi.45. Examples, possibly of this species, were also seen at Khandala in the Western Ghats and Malacca. Some of these specimens in life were pure apple green in colour, with little if any reddish brown markings (*cf.* Kimmins, p. 98), and it is just possible that this may represent the difference between *C. virens* Klapálek and this species.

Cloëon siccum sp. n.

Female imago (in life).—Whole body light sandy brown, abdomen cream underneath. Tails white. Legs translucent. Wings translucent colourless.

(In fluid.)—Head yellow; oculi black, ocelli mauve; antennae white. Thorax yellowish brown, mesonotum rather lighter. Abdomen orange yellow, greyer when empty of eggs; sternites cream. Tails white. Fore femur yellowish, rest of legs white, claws dusky. Proportions of hind tarsal joints, 9 : 4 : 3 : 7. Wings and veins colourless; all marginal intercalaries single and none posterior to Cu2; stigmatic area contains 5–7 close, simple, slanting veinlets.

Body length: Female 4–4½ mm. *Wing*: Female 4–5 mm.

India: Branch of the River Sonar, where it crosses the Saugor-Damoh road at the 12th milestone, C.P.

Three females were caught as duns at dusk on 11.iii.45. Day temperatures 80–85° F. Probably a dry season form. The duns have light grey wings.

This species is recognized by the small size, unpigmented wings and the uniform yellow colouring without distinctive markings. Banks' *C. pulchellum* would appear very similar to this, though probably differing in having "2–3 (cross veins) in the pterostigma, widely separated and two intercalaries behind median, cubitus and first anal." *C. variegatum* Chopra has characteristic thoracic markings.

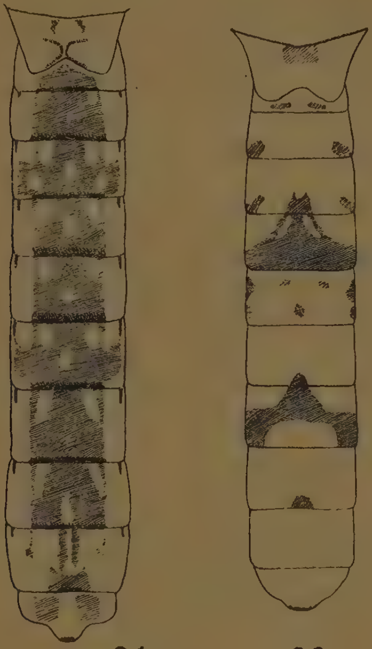
Cloëon septimum sp. n. (fig. 21, abdomen).

Female imago.—Head cream; oculi grey, ocelli white; antennae cream, basal segment with a reddish chocolate spot on the inner apical ring, distal segment ringed apically with the same colour (as in *C. bicolor*). Thorax cream; pronotum with faint red markings, metanotum with minimal red markings in the central area and a faint red lateral dot. Abdomen (fig. 21) cream with a central dorsal cherry red band, fading away on tergites 9–10 to a thin median line; on tergites 2–8 this central band has three or five pale dots on each segment and along the lateral margins of each of these tergites is a discreet red dash; on tergites 3 and 6, and to a lesser extent on tergite 8, the central band has broad lateral extensions; along the lateral margins of each of the first seven sternites is a broad longitudinal red line, slanting a little outwards and backwards. Tails white, with dark red joints. Legs white; fore femur reddish, mid and hind femora with a red subapical spot on the inner surface. Proportions of hind tarsal joints, 63 : 26 : 12 : 23. Wings vitreous, C and Sc area virtually colourless but with the very faintest milky tinge; base of radius and costal brace tinged with red, veins otherwise amber; stigmatic area contains two to three cross veins.

Body length: Female 4½ mm. *Wing*: Female 5 mm.

MALAYA: Batu Pahat, Johore.

The type female was captured as a dun at night in a house on 24.iv.46. Paratypes, three spent females found on the surface of a tank in the same locality, on 27.vi.46. A specimen, possibly a variant of this species, was found in Bangkok in January. It differs in being darker and browner in colour, in having femoral spots on the hind leg only, in the posterior margins of sternites 1–5 being dark red laterally and the pattern on the tergites being less distinctive.



FIGS. 21–22.—*Cloëon* species. (21) *C. septimum*, abdomen of ♀ imago, dorsum. (22) *C. julia*, abdomen of ♀ imago, dorsum.

This species is recognized by the absence of pigment in the wings, by the spots on the femora and by the characteristic markings on the abdomen, which distinguish it from other clear-winged species, though similar in this respect to *C. bengalense* Kimmins. *C. variegatum* Chopra has a characteristic variegated pattern on the thorax.

Cloëon julia sp. n. (fig. 22, abdomen).

Female imago.—A small, rather delicate fly. Head: Vertex orange; oculi black, rather prominent and squarish in lateral view; ocelli white; antennae white, basal and distal joints relatively longer and more slender than in the preceding species. Thorax generally cream; pronotum reddish along the posterior margin; mesonotum with two faint paramedian red lines; anterior portion of metanotum with a central dark red band. Abdomen (fig. 22) white; tergite 1 with a horizontal maroon line on either side of the mid line; on the lateral portions of tergites 2, 3, 5 and 7 are patches of the same colour spreading round, on tergite 7, to the mid line; tergite 4 almost wholly blood red, the colour overlapping in the mid line onto tergite 3; small patches of the same colour dorsally on 5, 6 and 7; along the lateral margins of tergites 2–8 is a thin intermittent maroon line; sternites unpigmented. Tails white. Legs white, fore femur with red spot at inner end, claws dusky. Proportions of hind tarsal joints, 20 : 6 : 2 : 6. Wings rather narrow, translucent colourless; veins colourless, except for the extreme base of radius and adjacent portion of costal brace, which are red; no marginal intercalaries behind first cubital interspace; stigmatic area contains one cross vein.

Body: Female 3½–4 mm. *Wing*: Female 4 mm. *Tail*: Female 6 mm.

MALAYA: Kluang, Johore.

One female was caught at dusk on the surface of a little sandy river, six miles from Kluang along the Mersing road, on 9.vii.46.

This species might be placed in the genus *Procloëon* on the grounds of the relative lengths of the hind tarsal joints. It was thought better, however, to leave the matter until further material was available. It is easily distinguished from other clear-winged species by the pigment on the abdomen, which is maximal on tergite 4, and to a lesser extent on tergite 7, by the absence of markings on the hind and mid-femora and by the white tails.

Procloëon bimaculatum (Eaton).

This species has been reported from a fairly wide area by previous authors, notably Ceylon, Eaton (1885) and Bengal, Kimmins (1947). It is possible that some of the reports of its occurrence in Indo-China, Java, Sumatra, the Philippines and Formosa may refer to *P. harveyi* Kimmins and further observations on this point are required. The nymph attributed by Ulmer (1939) to this species may also possibly belong to *P. harveyi*. It is interesting to note his description of the gills as "genau so gestaltet wie bei *Cl. simile* Etn.," suggesting that these two species might be placed in *Cloëon*, despite the proportions of the hind tarsi in the imago.

I have typical specimens from Bangalore, 19.xi.45, and Rangoon, 24.xii.45.

Procloëon harveyi Kimmins.

This species appeared to be much commoner than P. *bimaculatum*. Spent females were found at dawn in a jungle pool at Budni, Bhopal, on 14.iv.45, at Jhikargacha, W. Bengal, in July, at Poona in some numbers throughout August and September, and males were caught dancing in the early morning at Mirik, N. Bengal, at 4000 ft. in September. Outside India, females and males were caught in Bangkok in January, females probably of this species in Malacca and Batu Pahat in Malaya, and one very dried female in a cobweb at Fan Ling, in Hong Kong, on 15.iii.47.

Females of two clear-winged species, that might belong to this genus, were found in Central India, but they are not sufficiently well preserved now to warrant description.

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CONTENTS

PAGE

PARKER, ALEC H., Observations on the seasonal and daily incidence of certain biting midges (*Culicoides* Latreille—Diptera, CERATOPOGONIDAE) in Scotland . . . . 179–190, 2 figs.

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OBSERVATIONS ON THE SEASONAL AND DAILY INCIDENCE OF CERTAIN BITING MIDGES (*CULICOIDES* LATREILLE—DIPTERA, CERATOPOGONIDAE) IN SCOTLAND.

By Alec H. Parker.
(*Department of Zoology, University of Glasgow.*)*

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X 6

With 2 Text-figures.

Introduction.

That biting midges of the genus *Culicoides* Latreille are troublesome to man in most parts of Britain, and particularly so in Scotland, is well known. In this investigation, variations in the size and composition of the flying adult population occurring within the day and year are described. To obtain this information a series of standard collections was made over the greater part of the 1947 midge season at a site in the vicinity of Loch Lomond.

Seasonal, and, to a lesser extent, daily fluctuations in the incidence of *Culicoides* adults have also been investigated by Hill (1947), whose collections were made in Lancashire. Hill's methods differed in certain important respects from those used here, and will be discussed shortly. Seasonal variations in the incidence of some American *Culicoides* have been recorded by James (1943), again with a different method of collection. Among other recent observations those of Cameron, Downes, Morison and Peacock (1946, 1948), based on collections from many parts of Scotland, have proved of particular interest.

Although dealing mainly with daily and seasonal fluctuations in the flying midge population, this account includes sections on the influence of weather conditions on flying activity, and on the relative importance as man-biters of the species encountered.

In identifying *Culicoides* adults the specific descriptions of Edwards (1939) have been followed.

Method of Collection.

In making standard collections of *Culicoides* adults, James (1943) used a light trap. Hill (1947) utilized the attraction exerted by a black cloth. The efficiency of both methods seemed likely to vary with the light intensity of the environment; the attractiveness of a black cloth may well decrease, and that of a light trap increase, as daylight fades. If this is so, comparison of collections made at different times of day by either method must give a false impression of the relative abundance of midges at these times. A netting method, which did not depend on an active response by the insect, was therefore adopted.

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* Now at Department of Zoology, University of Nottingham.

It consisted in the execution of 400 strokes by the collector at about five feet above ground level. Probably its chief drawback was the variations which doubtless occurred in length of stroke, though the collector, who was always the same person, endeavoured to reduce this source of error to a minimum by standardizing his movements.

Collections were made along two closely defined " beats " in the vicinity of the Biological Field Station of the University of Glasgow. This is situated at the southern end of Rossdhu, on the west banks of Loch Lomond. One of the beats (Site A) ran about 100 yards along the edge of the loch, where there was a gap of 20–50 yards between the water's edge and fringing vegetation ; the latter consisted of sparsely placed alder and ash, with rhododendron in the shrub layer, and bracken predominating in the herb layer. Site A itself was stony and almost devoid of plant life, though some decaying vegetable debris was cast up from the loch. The second beat (Site B) followed a stream running through fairly open woodland for about 100 yards. It was 100–200 yards from Site A. The vegetation at and around Site B consisted chiefly of oak, ash, and beech, in the tree layer, birdcherry and rhododendron in the shrub layer, with bracken again dominating the herb layer.

Each time a standard collection was made, 400 strokes with the net were executed, first at Site A, then at Site B. The midges captured were removed by means of an aspirator after the first set of strokes, and again after the second set, the two collections being kept separate. Each set of strokes, together with the subsequent removal of midges from the net, occupied 5–10 minutes.

The elimination of variations in weather conditions proved very difficult. As far as possible, collections were made on warm days when there was little or no wind. Sudden changes frequently occurred, however, and many collections had to be made under conditions which could not be so described. Weather conditions at the time of each collection were therefore recorded.

In the account which follows, data are, for the most part, given separately for each species. The one exception to this concerns *C. obsoletus* Meigen and related forms, a group comprising *C. obsoletus* Meigen, *C. chiopterus* Meigen, and, according to the observations of J. A. Downes (*unpublished data*), two other species. All these forms are readily separable in the male, but not in the female. Adults of any of these species will therefore be alluded to as being of the *C. obsoletus* group. Under the heading of *C. pulicaris* L. will be included individuals, both of typical *C. pulicaris*, and of *C. pulicaris* var. *punctatus* Meigen.

SEASONAL VARIATION.

To determine variations in the flying midge population occurring during the course of a season at Rossdhu, collections were made at intervals from the beginning of June until almost the end of October, 1947. Flying *Culicoides* adults were first observed in mid-May, but were present only in very small numbers during this month. By the end of October numbers had diminished almost to vanishing point.

As will be shown in the next section, the time of day at which maximum numbers of adults were captured varied with sex and species. Hence, to compare the incidence of different sexes and species through the season, it was desirable to consider each at the particular time of day at which greatest numbers were obtained. Even for a single sex and species, however, this time varied on different days. It has therefore been thought advisable to record, for each sex of each species, the highest number of adults captured in any single collection during the course of any given evening. This has been done in Table I. Since collections were usually made at intervals of an hour or less, one, at least, was likely to have been made fairly near to the time at which each sex and species was in maximum flight. The figures shown in Table I can therefore reasonably be regarded as an approximate index of relative abundance.

TABLE I.—*The Seasonal Incidence of* Culicoides *Adults at Rossdhu, as Indicated by the Greatest Numbers of Each Sex of Each Species Obtained per Standard Collection on Different Evenings.*

Date of collection.	*C. impunctatus.*				*C. pallidicornis.*				*C. heliophilus.*				*C. obsoletus* grp.				*C. pulicaris.*			
	Site A.		Site B.		Site A.		Site B.		Site A.		Site B.		Site A.		Site B.		Site A.		Site B.	
	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂
June 2	0	0	1	0	0	0	0	0	0	0	0	0	3	0	3	3	1	0	1	4
„ 6	2	1	2	0	0	0	0	0	0	0	0	0	1	0	1	1	1	1	1	5
„ 11	0	0	2	0	0	0	0	5	2	0	0	0	1	0	1	0	0	0	2	0
„ 19	19	0	5	1	0	2	2	83	6	1	2	0	2	0	1	0	0	0	0	4
„ 25	10	0	8	0	1	4	12	255	29	1	8	1	4	1	0	0	0	0	0	0
July 1	38	1	25	0	40	5	120	83	7	0	2	0	1	0	3	0	1	1	0	1
„ 9	11	2	9	1	1	2	96	169	3	0	2	0	5	0	0	0	0	0	2	12
„ 17	12	6	26	1	8	4	130	73	1	0	0	0	4	2	0	0	0	12	0	2
„ 24	3	0	11	0	4	1	35	93	1	0	0	0	1	1	0	0	1	7	0	9
„ 30	2	0	18	0	3	20	53	85	0	0	0	0	2	1	2	0	0	8	0	13
Aug. 4	9	0	3	1	1	21	18	112	0	0	0	0	4	0	4	1	1	3	0	2
„ 24	1	0	1	1	1	0	3	41	0	0	0	0	2	0	1	0	0	1	0	5
„ 30	0	0	2	0	0	0	1	12	0	0	0	0	1	0	1	0	0	0	0	12
Sept. 6	0	0	0	0	0	2	0	3	0	0	0	0	7	0	8	0	0	1	0	7
„ 17	0	0	0	0	0	0	0	0	0	0	0	0	2	0	1	0	2	0	0	1
„ 21	0	0	0	0	0	0	0	0	0	0	0	0	2	0	1	0	1	1	0	0
Oct. 1	0	0	0	0	0	0	0	0	0	0	0	0	1	2	9	0	0	0	1	0
„ 12	0	0	0	0	0	0	0	0	0	0	0	0	6	0	3	0	2	1	1	0
„ 17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
„ 23	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0
Totals	107	10	113	5	59	61	470	1014	49	2	14	1	50	7	40	5	10	36	8	77

It will be noticed that in three species—*C. impunctatus* Goetghebuer, *C. pallidicornis* Kieffer and *C. heliophilus* Edwards—a moderately well defined peak in abundance occurred and no adults were captured over much of the collecting period. The adult seasons of the first two were almost identical; both reached a maximum in early July, and both were obtained over approximately the same period—*C. impunctatus* from the beginning of June to the end of August, *C. pallidicornis* from early June to early September. The adult season of *C. heliophilus* (early June to late July) was rather shorter, and the peak (late June) a little earlier. *C. obsoletus* group and *C. pulicaris* adults were obtained in small numbers from June to October, and such numerical fluctuations as there were seem of doubtful significance. These species were also captured in mid-May; no other members of the genus were captured before June.

Since the species constituting the *C. obsoletus* group were distinguishable in the male, an indication of the seasonal incidence of each was obtained by noting their occurrence among the male population at different times of year. From collections made at Rossdhu and in Glasgow, it appeared that all four species were present both at the beginning and the end of the adult midge season.

As reference to Table I will show, the midge populations at Sites A and B displayed certain differences, the most consistent and well defined of which were that *C. pallidicornis* was more abundant at Site B, and *C. heliophilus* more abundant at Site A.

It will also be seen from Table I that the male : female ratio of the adults captured varied greatly in different species. Percentage sex-ratios calculated from the totals given in Table I were, in fact, as follows :

C. impunctatus (235 specimens), 94 per cent ♀ ; *C. pallidicornis* (1604), 33 per cent ♀ ; *C. heliophilus* (66), 95 per cent ♀ ; *C. obsoletus* group (102), 88 per cent ♀ ; *C. pulicaris* (131), 14 per cent ♀.

The species so far mentioned were the only ones obtained in moderate or large numbers at Rossdhu. Other species captured were *C. fascipennis* Staeger, *C. cunctans* Winnertz, *C. odibilis* Austen, and *C. grisescens* Edwards, but since not more than five individuals of any of these species were obtained during the whole season, little is to be gained from discussion of their times of capture.

Daily Variation.

It was expected that fluctuations in the number of flying midges occurring within a single day would bear a fairly constant relationship to the times of sunset and sunrise. This was found to be so ; between June and October the relative lengths of day and night altered by several hours, but the evening flight always occurred at approximately the same time in relation to sunset.

Three sets of collections, made in early July, late July, and late August, were started in the early afternoon, continued through the night, and on into the following morning. For the most part there were hourly intervals between successive collections. Maximum numbers were invariably obtained between just over three hours before, and one hour after, sunset. During the night few or no midges were captured, following which there was a slight increase at sunrise ; this morning flight was always on a very much smaller scale than that of the previous evening. Shortly after sunrise, numbers again diminished almost or quite to vanishing point, and remained so until evening. These facts can be seen at a glance from fig. 1, in which the results of one of the sets of collections are plotted. (As will be seen shortly, the double evening peak shown in this figure was due to the habits of *C. pallidicornis*, the most abundant species at the time of collection.)

So far, the daily incidence of all species and both sexes has been considered collectively. In Table II the limits between which lay the times of collections yielding the greatest numbers of each sex and species on different evenings are shown. The collections on which these data are based were made at frequent intervals, usually of one hour or less, and at both sites. Sometimes only one or two adults of a particular type were captured during an entire evening, so that the times at which maximum numbers were captured are of little significance. Because of this, times of maximum flight based only on sets of collections in which the greatest number captured was at least five are also shown.

It will be noticed that maximum numbers were usually captured at or around sunset. To this there were two conspicuous exceptions—*C. heliophilus* females and *C. pallidicornis* males—both of which reached a maximum several hours earlier. Of species captured in greatest numbers around sunset, the maxima showing least variation in time of occurrence were those of *C. pallidicornis* females and *C. pulicaris* males ; when the maximum number captured was not less than five, the peak for these species occurred at, or shortly after,

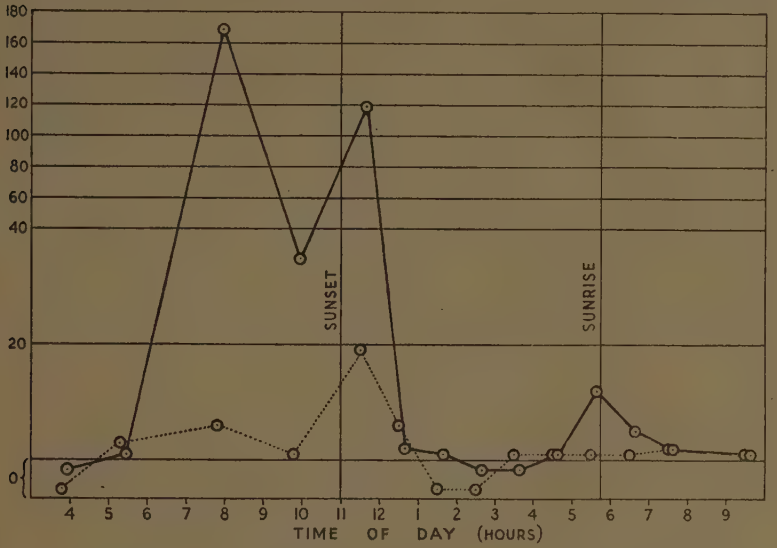

Fig. 1.—The incidence of *Culicoides* adults at Rossdhu, 9th–10th July, 1947. Unbroken lines : Site A ; stippled lines : Site B.

Table II.—*The Times of Maximum Flight of* Culicoides *Adults at Rossdhu, as Indicated by the Times of Collections Yielding the Greatest Numbers of Each Sex and Species on Different Evenings.*

Times are expressed in relation to sunset :
e.g. 0·00 = sunset.
+ 1.00 = 1 hour after sunset.
– 1.30 = 1 hour 30 min. before sunset.

n = Number of sets of collections on which the figures are based.

Species.	All collections.						Collections comprising five or more adults.					
	Females.			Males.			Females.			Males.		
	From.	To.	n.	From.	To.	n.	From.	To.	n.	From.	To.	n.
C. impunctatus	– 2·00	+ 1·00	23	– 8·20	+ 1·30	9	– 1·30	+ 1·00	13	—	—	0
C. pallidicornis	– 2·20	+ 1·00	18	– 5·00	– 0·30	21	0·00	+ 0·40	9	– 5·00	– 1·20	14
C. heliophilus	– 5·40	– 0·40	11	– 5·40	– 2·20	3	– 5·40	– 2·00	4	—	—	0
C. obsoletus grp	– 5·00	+ 1·20	34	– 2·20	+ 0·20	8	– 1·10	+ 0·30	5	—	—	0
C. pulicaris	– 3·10	+ 0·40	14	– 1·00	+ 1·00	23	—	—	0	– 0·10	+ 1·00	10

sunset. The maxima of *C. impunctatus* females and *C. obsoletus* group females varied from shortly before to shortly after sunset, but it must be noted that *C. obsoletus* group females were obtained only in small numbers.

It is evident from Table II that males and females of *C. pallidicornis*—the only species of which both sexes were obtained in large numbers—behaved very differently. This difference is shown strikingly in fig. 2, in which the numbers of males and females of this species captured during three complete sets of collections (i.e. on three different evenings) are plotted in full. A further point of interest concerning *C. pallidicornis* males is that they were observed to be dancing in swarms. This phenomenon, which we have also observed in males of *C. grisescens* Edwards, appears to have been previously recorded for *Culicoides* only by Goetghebuer (1919), who observed it in males of *C. pulicaris*.

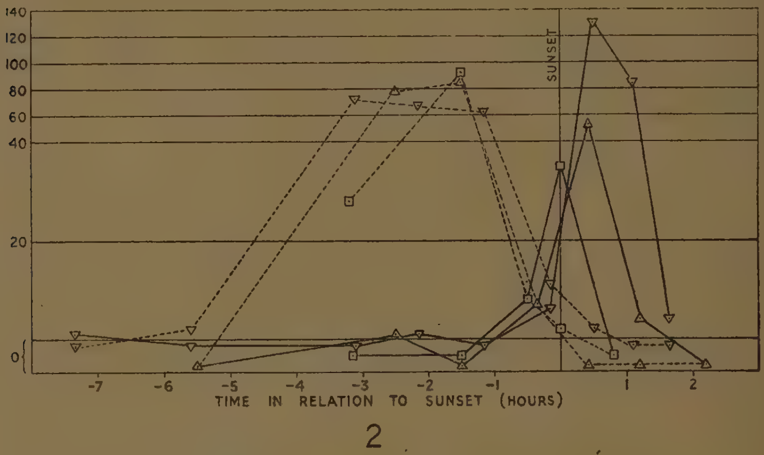

Fig. 2.—The incidence of *C. pallidicornis* at Rossdhu on three different evenings. Unbroken lines: females; broken lines: males.

Influence of Weather Conditions.

It has been mentioned that a certain degree of variation in the weather conditions under which collections were made was unavoidable. Since conditions prevailing at the time of each collection were recorded, it seemed that information on their effect on the activity of flying midges might be obtained. The conditions recorded were temperature, humidity (measured by a whirling hygrometer), strength of wind, strength of rain, and light intensity (subjective estimates).

Wind.—Wind had a very pronounced effect; a sudden increase in its strength always resulted in an equally sudden diminution in the number of flying midges captured. Collections made during strong winds never yielded any adults.

Temperature.—There was no apparent correlation between temperature and numbers captured, but since the effect of other weather conditions could rarely be eliminated, direct comparison of catches was seldom permissible. It may be noted that large numbers were captured at all temperatures from 10–20° C.

Humidity.—There was no apparent correlation between either relative humidity or saturation deficiency and numbers captured. As with temperature, directly comparable data were scarce. Large numbers were captured at relative humidities ranging from 60–95 per cent., and at saturation deficiencies of 0·5–6·0 mm.

Rain.—The few collections made during soft rain yielded almost the same numbers of midges as otherwise comparable collections made when rain was not falling.

Light intensity.—The light intensity at any given time relative to sunset varied from day to day, depending on the degree to which the sun was obscured by clouds. To test the effect of these variations on the time of maximum flight, the data in Table II were split up according to whether the sun was visible ("bright") or obscured by clouds ("dull") at the time of collection. Table III shows the results of this procedure; only species of which fairly large numbers were captured, and only sets of collections in which the maximum number captured was at least five, have been considered. It will be noticed that the mean time of maximum flight was invariably earlier on dull than on bright days. It is highly probable that so consistent a result is significant, though the degree of overlapping between the two sets of data, together with the small numbers of collections on which they are based, makes confirmation desirable.

Table III.—*The Times of Maximum Flight of* Culicoides *Adults at Rossdhu on Dull and Bright Evenings, as Indicated by the Times of Collections Yielding the Greatest Numbers of Each Sex and Species.*

Only collections comprising five or more adults are included. Times are expressed in relation to sunset (see Table II). n = Number of sets of collections on which the figures are based.

Species.	Dull evenings.				Bright evenings.			
	From.	To.	Mean.	n.	From.	To.	Mean.	n.
C. impunctatus ♀♀	– 1·30	– 1·10	– 1·20	3	0·00	+ 1·00	+ 0·25	10
C. pallidicornis ♀♀	0·00	+ 0·20	+ 0·10	3	0·00	+ 0·40	+ 0·20	6
C. pallidicornis ♂♂	– 4·30	– 1·30	– 3·25	5	– 3·40	– 1·20	– 2·40	9
C. pulicaris ♂♂	– 0·10	0·00	0·00	4	0·00	+ 1·00	+ 0·30	6

Attraction to Man.

During the evenings on which collections were made, the writer periodically sat outside, exposing arms and face, and, with the aid of a mirror, captured all midges landing. Comparison of *Culicoides* adults so captured with those on the wing, as indicated by standard hand-net collections made shortly before and afterwards, provided a rough means of comparing the degree to which different species were attracted to man. The exposures were for 15 minutes, and were done either at Site A, or, more frequently, at Site B.

Table IV shows, for each of the species previously dealt with, the numbers attracted during five exposures. The exposures selected for presentation are those which yielded the greatest numbers of each species. (Some species were attracted during fewer than five exposures, and several zeros therefore appear in the table.) Beside these figures are shown estimates of the numbers of adults which would have been obtained in standard hand-net collections (i.e. of 400 strokes) had they been made at the same time. Hand-net collections were often made immediately before and after the exposure, in which case the figure given is the mean of the two collections. At other times they were made up to an hour before or after exposure, and here the figure quoted is derived from a graph in which the results of the collections were plotted. The data refer exclusively to females; males, so far as our observations go, are not attracted to man.

Table IV shows *C. impunctatus* females to have been very much more strongly attracted to man than any other species for which records were obtained. Among other species, no well defined differences of this nature were displayed.

TABLE IV.—*The Numbers of Female* Culicoides *Attracted to Man During* 15-*minute Exposures Compared with the Estimated Numbers of Flying Females per Standard Collection.*

Times are expressed in relation to sunset (see Table II).

Species.	Date.	Time at which exposure started.	Estimated number of flying females per standard collection.	Number of females attracted.	Females attracted / Flying females.
C. impunctatus	July 17	+ 0·45	11	24	2·2
	„ 17	0·00	4	13	3·2
	„ 30	0·00	16	124	7·8
	Aug. 4	+ 0·30	8	55	6·9
	„ 30	– 0·25	0	19	19·0 +
		Totals	39	235	6·0
C. pallidicornis	June 25	– 2·30	1	1	1·0
	July 17	0·00	6	0	0·0
	„ 17	+ 0·45	5	0	0·0
	„ 30	0·00	30	21	0·7
	Aug. 4	+ 0·30	1	0	0·0
		Totals	43	22	0·5
C. heliophilus	June 19	– 3·00	4	1	0·3
	„ 25	– 5·00	20	16	0·8
	„ 25	– 3·00	10	4	0·4
	July 1	– 3·00	3	1	0·3
	„ 17	– 1·30	1	0	0·0
		Totals	38	22	0·6
C. obsoletus grp.	June 2	– 1·00	3	1	0·3
	„ 25	– 3·00	3	1	0·3
	Sept. 6	– 0·15	3	1	0·3
	Oct. 1	– 1·00	4	1	0·3
	„ 12	– 1·30	5	4	0·8
		Totals	18	8	0·4
C. pulicaris	June 2	0·00	1	0	0·0
	„ 6	– 2·25	1	0	0·0
	Aug. 4	+ 0·30	1	0	0·0
	„ 24	+ 0·30	1	0	0·0
	Oct. 12	– 1·30	2	1	0·5
		Totals	6	1	0·2

It may be mentioned that two species of which previous human biting records are rare have been observed biting in large numbers. One is *C. grisescens* Edwards, observed to attack man at Auchterawe, Invernesshire, in September, and the other, *C. halophilus* Kieffer, which in July was an intolerable pest at Arrochar, Dumbartonshire.

Discussion.

It is interesting to compare the Rossdhu collections with collections made elsewhere in Britain. Those of Cameron *et al.* (1946, 1948) were made over many parts of Scotland, chiefly by the use of a hand-net. The collections of Hill (1947) were more systematic, and were made at a site in Knowsley Park, Lancashire. Hill collected on still evenings at fairly regular intervals from the end of March to the beginning of November, 1945. Her method was to capture all *Culicoides* adults alighting on a black cloth between two and one hours before sunset. Males were not attracted, and no data on their incidence are given.

Hill obtained *C. impunctatus* from the beginning of May until early August, observing a peak in June. This is rather earlier than the times recorded at Rossdhu. The difference may have been due partly to the exceptionally prolonged cold spell of early 1947, but since Cameron *et al.* (1946) record the 1945 *C. impunctatus* season in Scotland as having been roughly identical with that observed at Rossdhu in 1947, the difference is probably more an expression of a general tendency for times of emergence to be later in northern than in more southern parts of Britain.

As at Rossdhu, Hill observed *C. obsoletus* adults to be present through the entire midge season. She found two definite peaks in abundance, and from this, and from evidence based on the emergence of adults in captivity, considers that *C. obsoletus* passes through two generations per annum. Edwards (1939) and Cameron *et al.* (1948) have expressed the same view. There is little indication of a double peak in adult abundance from the Rossdhu collections, but numbers captured here were at all times small.

C. pallidicornis occurred only in very small numbers in Hill's collections, exclusively between mid-June and mid-July, i.e. slightly earlier than, but overlapping into, the time at which maximum numbers of this species were captured at Rossdhu. *C. pulicaris* was obtained only once—in September—but Goetghebuer (1919) states that this species is found in Belgium from spring to autumn, thus indicating a prolonged adult season similar to that observed at Rossdhu. The same author's statement that *C. pulicaris* passes through several generations per annum receives no support from the findings at Rossdhu, but numbers obtained here were small. Hill did not obtain *C. heliophilus*, but Cameron *et al.* (1948) state this species to be a " vigorous biter in late June," the time at which the peak occurred at Rossdhu. Cameron *et al.* also state that *C. heliophilus* probably passes through two generations per annum. The Rossdhu collections give no indication of this; *C. heliophilus* adults were obtained only in June and July, and during this time reached a single, well defined, peak.

Judging from the collections of Cameron *et al.* (1946), the commonest species of *Culicoides* over most of Scotland is *C. impunctatus*; the predominance of *C. pallidicornis* at Rossdhu appears to be exceptional. Excluding *C. pallidicornis*, the relative abundance of the different species captured at Rossdhu seems to have been roughly equivalent to their relative abundance over much of Scotland, though *C. grisescens* and *C. fascipennis* are apparently very much more abundant in many localities.

The explanation for the abnormal sex-ratio of most species captured at Rossdhu is not known, but the following observations are relevant : (*a*) Cameron *et al.* (1946), while normally obtaining a preponderance of females in collections of *C. impunctatus*, occasionally captured males and females in approximately equal numbers ; (*b*) Hill (1947) found the proportions of males and females of *C. impunctatus* emerging from pupae obtained in the field to be roughly the same ; (*c*) *C. obsoletus* group adults observed resting on trees consisted of males and females in approximately equal numbers. Thus it seems likely, as Cameron *et al.* suggest for *C. impunctatus*, that males of this species and the *C. obsoletus* group " have some unrecognized habit which makes them difficult to collect by the methods usually employed." Such a habit might be a tendency to rest among the vegetation rather than engage in flight, or to fly at higher levels than those explored by the hand-net. Similar habits might account for the scarcity of *C. heliophilus* males and *C. pulicaris* females.

The tendency for *Culicoides* females of most species to be present in greatest numbers in collections made at or around sunset was consistent with the well-known fact that biting is worst at this time. Numbers were also expected to fall off during the night, though in view of Edwards' (1939) statement that biting continues throughout the night in sultry weather, the extent to which they did so was surprising. The wide difference between numbers captured at sunset and sunrise was also unexpected. There was no obvious difference in weather conditions to account for it, though each time it was slightly colder at sunrise than at sunset. Hill (1947), who also made a collection at sunrise, similarly obtained small numbers in comparison with those she was obtaining during evening collections. Thus the generalization that the morning flight is normally on a smaller scale than the evening flight seems justified.

The few continuous collections, extending over several hours, made by Hill, gave results not at first sight consistent with those presented here. As at Rossdhu, practically no *C. impunctatus* or *C. obsoletus* group females were obtained in full daylight, but the size of her catches increased only up to half an hour before sunset. After this there was a fairly steep drop. It seems likely that this drop was a result of the collecting technique employed, rather than of a decline in the number of flying midges. As Hill points out, the attraction exerted by a black cloth may well diminish as light fades.

C. heliophilus females differed from females of other species obtained at Rossdhu in having been captured in greatest numbers several hours before sunset. The daytime activity of this species has previously been noted by Edwards (1939), who named it accordingly. Apparently *C. heliophilus* is not the only British species in which the female behaves in this way ; Steward (1933) observed that females of *C. nubeculosus* Meigen bit in greatest numbers around mid-day.

It is difficult to understand what advantage the several hours difference between the times of maximum incidence of males and females of *C. pallidicornis* can confer on the species. It is conceivable that the time of maximum incidence of the females is associated with the availability of their hosts—possibly crepuscular mammals. The male swarms, on the other hand, are probably directed towards mating, which may involve a visual mechanism, and require a certain light intensity for its effective performance. But until more evidence is available such suggestions must remain conjectural.

The pronounced effect of wind upon the activity of *Culicoides* adults observed at Rossdhu is corroborated by several authors. It has been noted by Bequaert (1924), Painter (1926) and Myers (1935), in the West Indies, and by Hill (1947) at Knowsley. It has several times been either stated or implied that a moderately high temperature is necessary for the attainment of maximum flying activity, one of the most definite pronouncements being that of Myers (1935), who says " for full activity, *C. furens* apparently needs about 80° F." No experimental evidence is given in support of this statement, and it seems that the influence of temperature on the activity of *Culicoides* adults has yet to be demonstrated. No reference to the effect of humidity differences on activity has been found, but the observation that gentle rain had no obvious effect on numbers captured is corroborated by Hill (1947), who says " drizzling rain does not deter the activities of *C. impunctatus*."

It has been shown that the evening and morning flights of *Culicoides* adults regularly recur at approximately the same times in relation to sunset and sunrise. It may be that some internal rhythm is involved in this recurrence, but it is difficult to see how it can by itself be responsible for such behaviour when the relative lengths of day and night are continually changing. Of the variables measured, only light intensity was related to numbers captured at all times of day in a way suggesting that it served as an operative stimulus. That it did so is borne out by the observed tendency for the evening flight to occur earlier on darker than on lighter evenings.

That *C. impunctatus* is exceptionally strongly attracted to man is corroborated by both Cameron *et al.* (1946) and Hill (1947). *C. pallidicornis*, *C. heliophilus*, *C. pulicaris* and the *C. obsoletus* group, of which smaller numbers were attracted at Rossdhu, have all at some time, as Edwards (1939) relates, been described as troublesome pests.

SUMMARY.

Systematic collections of Culicoides made with a hand-net at a site on the shore of Loch Lomond, showed the seasonal incidence of species obtained in moderate or large numbers to be as follows : *C. impunctatus*, June–August (peak period, July) ; *C. pallidicornis*, June–September (July) ; *C. heliophilus*, June–July (late June) ; *C. pulicaris*, *C. obsoletus* group, May–October (no well defined peaks).

The sex-ratios of these species were always unequal ; in some species females were the more numerous sex, in others, males. Only *C. pallidicornis* yielded large numbers of both sexes.

Culicoides adults were obtained in greatest numbers during the evening. Apart from a small increase at sunrise, they were almost completely absent at other times. The evening peak of *C. pallidicornis* ♀, *C. impunctatus* ♀, *C. obsoletus* group ♀, and *C. pulicaris* ♂, was around sunset, that of *C. pallidicornis* ♂ and *C. heliophilus* ♀ several hours earlier.

The number of adults captured was very much affected by wind strength, but the temperature and humidity differences encountered had no apparent effect. The time of evening flight, relative to sunset, tended to be earlier on darker than on lighter evenings.

A series of exposures showed that *C. impunctatus* females were much more strongly attracted to man than females of the other species mentioned above.

The observations made are discussed in relation to those of other investigators.

ACKNOWLEDGEMENTS.

This investigation is part of a research programme made possible by the generosity of Sir Harold Bowden, Bt., and carried out under the general direction of Mr. J. A. Downes, Lecturer in Entomology, University of Glasgow. The late Sir Iain Colquhoun, Bt., of Luss, kindly gave permission for collections to be made on his estate at Rossdhu. I am indebted to Mr. D. S. Kettle for his helpful criticism of the draft manuscript.

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CONTENTS

PAGE
PAGDEN, H. T., M.A., F.R.E.S. Descriptions and records of Austro-Malaysian METHOCIDAE and MUTILLIDAE (Hymenoptera) . . 191–231, 14 figs.

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DESCRIPTIONS AND RECORDS OF AUSTRO-MALAYSIAN METHOCIDAE AND MUTILLIDAE (HYMENOPTERA).

By H. T. Pagden, M.A., F.R.E.S.

(Manuscript received 31st August, 1948.)
(Read 1st June, 1949.)

With 14 Text-figures.

Contents.

PAGE
Introduction 192
Descriptions
Key to Malayan species of *Methoca* 194
Methoca malayana sp. n. 195
Methoca penthesilea sp. n. 196
Timulla (*Trogaspidia*) *erato* Mickel and related species . . . 198
Key to Males 199
T. (*T.*) *erato* Mickel 200
T. (*T.*) *selene* sp. n. 200
T. (*T.*) *mickeli* sp. n. 201
T. (*T.*) *stephani* (Magretti) 204
T. (*T.*) *sceva* (Cameron) 205
T. (*T.*) *sondaica* sp. n. 208
T. (*T.*) *philippinensis* group 210
Key to Males 210
Key to Females 211
T. (*T.*) *philippinensis philippinensis* (Smith) 212
T. (*T.*) *philippinensis singapora* Mickel 212
T. (*T.*) *philippinensis malayana* (Cameron) 212
T. (*T.*) *philippinensis sunda* Mickel 213
T. (*T.*) *philippinensis kangeana* subsp. n. 214
T. (*T.*) *philippinensis paloeana* subsp. n. 215
T. (*T.*) *philippinensis sumbana* subsp. n. 216
T. (*T.*) *bataviana* (André) 217
Smicromyrme kellyi Pagden, new synonymy 218
S. athalia sp. n. 219
S. decora (Smith) female redescribed 223
S. decora (Smith), male described 224
Records:
Squamulotilla deserta (Smith) 225
S. aesyca (Cameron) 226
Odontomutilla familiaris familiaris (Smith) 226
O. haematocephala (André) 226
O. herpa (Cameron) 227
O. manifesta (Smith) 227
O. rubrocapitata Mickel 227
O. thymele Mickel 227
O. urania (Smith) 228
O. cassiope (Smith) 228
Timulla (*Trogaspidia*) *celebensis* (André) 228
T. (*T.*) *amans amans* (André) 228
T. (*T.*) *amans oryzae* Pagden 229
References 229

INTRODUCTION.

In publishing this paper I wish to record my thanks to Professor Clarence E. Mickel, of the University of Minnesota, for encouragement to continue my investigations, and to the following for the loan of numerous specimens: Dr. J. van der Vecht, Instituut voor Plantenziekten, Buitenzorg, Java; Dr. J. G. Betrem, Malang, Java; Dr. M. A. Lieftinck, Director, Zoologisch Museum, Buitenzorg, Java; the late Mr. H. M. Pendlebury, Director, F.M.S. Museums, Kuala Lumpur, Federated Malay States; Professor Dr. Oscar de Beaux, Director, Museo Civico di Storia Naturale, "Giacomo Doria," Genoa, Italy; the authorities of the Leyden Museum; and the authorities of the British Museum (Natural History).

For testing my keys I am indebted to the late Mr. H. M. Pendlebury, Mr. N. C. E. Miller, previously entomologist in the Department of Agriculture, Kuala Lumpur, Federated Malay States, and to Mr. M. W. F. Tweedie, Director Raffles Museum, Singapore.

The species herein recorded or described form only a very small part of the collections which have been so generously sent to me for examination. The vast bulk of the material is composed of species, mostly of *Trogaspidia* and *Smicromyrme*, which are undescribed, difficult to separate, and even more difficult to fit into a logical and simple key.

It will be realized that the time required for a critical survey of some thousands of specimens, most of them, as already indicated, belonging to undescribed species, is great, and as the time at my disposal is limited, it is likely to be some years before the material can be properly worked out. I have, therefore, thought it better to publish the results of my investigations in a series of short papers, to avoid confusion over specimens already bearing determination labels and returned to individuals or institutions, rather than to wait until I can publish a complete survey of all the known species of the Malaysian region. In the event this has not proved possible, for the Pacific War prevented publication, and many types and paratypes had already been returned to the collections whence they came.

In this paper I have added three new subspecies to the *philippinensis* group of *Timulla* (subgenus *Trogaspidia*), and have also described the female of *T.* (*T.*) *philippinensis sunda* Mickel. The species *T.* (*T.*) *erato* Mickel, previously considered to be unique in the possession of a spatulate calcar on the anterior tibia, is now found to belong to a group of species which exhibit both this character and the peculiar form of the median area of the clypeus described by Mickel. I have termed this the *erato* group and have divided it into two distinct sub-groups: that with a single carina on the antennal scape beneath, and that with the scape bicarinate beneath. I have considered the representatives as specifically distinct, though some are very closely related, as shown by the similarity in the male genitalia, but differences in the pubescent markings are considerable.

I have made *T.* (*T.*) *oryzae* Pagden a subspecies of *amans* (André). I can find no differences in the male genitalia of these insects, nor is there any difference in structure, though there are small differences in sculpture and pubescence.

In the genus *Smicromyrme* the male of *decora* (Smith) is described for the first time. Some biological notes on this insect will be found in 1934, *J. F.M.S. Mus.* **17** : 465. *Smicromyrme athalia* is a new species. The association of the sexes is not entirely certain and is based on the occurrence of males and females at the same time and in the same locality, even to being taken on the same shrub, on several occasions.

Records and redescriptions of certain other species are included.

As regards the keys to the subspecies of *philippinensis* and to the *erato* group, I have endeavoured to use only such characters as are readily appreciated and obvious. When in their final form these keys were successfully used for the separation of the material on which they were based, after substituting numbers for the names, by some of my colleagues who have no specialized knowledge of the MUTILLIDAE.

When the Pacific War started, the author was mobilized with the Malayan Volunteer Air Force, and on the fall of Singapore the manuscript was written off as a loss. Two friends, however, preserved both the original and the carbon copy. The original was in the Selangor Museum, awaiting publication and, after many vicissitudes, was returned to me by Enche Bachik bin Mohamed Tahir, the clerk and caretaker. The carbon copy was rescued by my assistant and friend, Enche Kamarudin bin Bahar, of the Department of Agriculture, who found it among some 1300 papers on Hymenoptera lying on the floor in the Department. Both original and carbon were returned to me early in November, 1945. I take this opportunity of recording my deep gratitude to both the friends mentioned above.

METHOCIDAE.

Methoca Latreille.

In an earlier paper, 1934, *J.F.M.S.Mus.* **17** : 454, I followed André (1903, *Genera Insectorum* **11**) and included *Methoca* in the MUTILLIDAE, but I feel that there is little doubt that it should be placed in a separate family, as has been done by several authors. I cannot subscribe to the view that it should be included in the THYNNIDAE, a family confined, with the single exception of California, to Australia, Tasmania, and New Zealand including the Pacific Islands, and South America. Apart from the fact that *Methoca* does not occur in Australia and the THYNNIDAE, unless we include *Methoca*, do not occur in Europe, N. America and Africa, the structure of *Methoca* is so different from that of the THYNNIDAE that there seems no valid reason even to consider it as a candidate for admission to that family. Similarly, on morphological grounds, it seems desirable to remove it from the MUTILLIDAE.

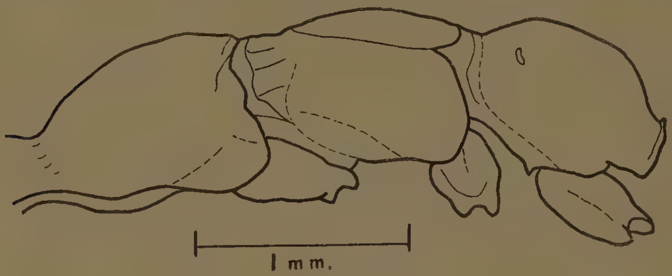
In Malaya there are four known species of *Methoca*, two of them described for the first time in this paper. Each cf these is based on a single female only, but they are so different from the other Malayan species known in that sex, *M. violaceipennis* Cameron, that I feel that their occurrence should be placed on record.

The Malayan species of *Methoca* are easily separable by means of the following key :

Key to the Malayan species of *Methoca*.

Females.

1. Head, viewed from above in the plane of the ocelli, concave between the eyes, without facial protuberances, strongly receding behind the eyes . . . *penthesilea* sp. n.
   Head not as above . . . . 2.
2. Frons acutely bi-tuberculate above the line of antennal insertion, longitudinally micro-rugulose. Thorax with only the scutellum of the mesonotum convex. Eyes pubescent . . . *violaceipennis* Cameron.



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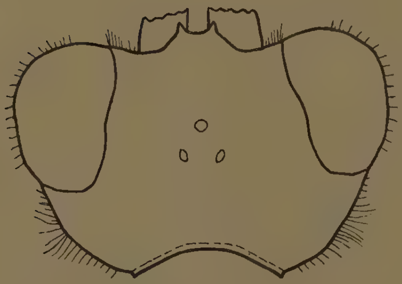

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Figs. 1–2.—(1) Side view of thorax of *Methoca violaceipennis* Cameron, ♀; (2) Dorsal view of head of *M. violaceipennis* Cameron, ♀.

Frons swollen medially above the antennae, bi-tumescent, but not bi-tuberculate, polished and shining, with scattered punctures. Scutum and scutellum of mesonotum convex. Eyes glabrous . . *malayana* sp. n.

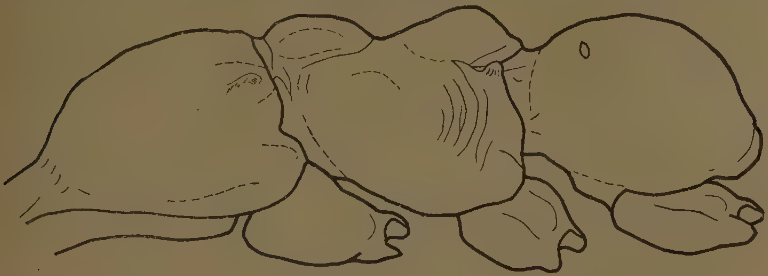
Males.

Clypeus, viewed laterally, with a strong, spinose tubercle at the base. Propodeon strongly reticulate . . . . *clypeata* Pagden

Clypeus, viewed laterally, at most with a median, carinate elevation. Propodeon rugulose, feebly reticulate basally . *violaceipennis* Cameron.

Methoca malayana sp. n.

♀. Head and abdomen, except the basal and apical abdominal segments, black ; thorax ferruginous ; last six segments of antennae piceous, the scape pedicel and four basal flagellar segments ferruginous ; mandibles castaneous ; legs mainly dark, except the coxae, ferruginous ; head, thorax and abdomen with scattered, erect, piceous setae which are mainly disposed dorsally, genae and gular region of head, underside of thorax and abdomen, and the legs, with sparse, fine, pale pubescence. Frons above the antennae swollen, bitumescent ; clypeus with a median, polished tumescence, the distal half subnitent, transversely micro-striate, anterior margin transverse ; mandibles castaneous, piceous at the base externally, with a well-developed keel on the face extending from the base to the pre-apical tooth. First tergite with a latero-dorsal castaneous suffusion ; first sternite ferruginous on apical half.



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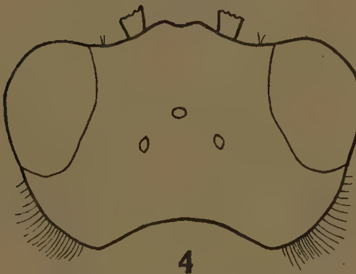

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FIGS. 3–4.—(3) Side view of thorax of *Methoca malayana* sp. n., ♀ ; (4) Dorsal view of head of *M. malayana* sp. n., ♀.

Length : 7 mm.

Head black, highly polished, with moderate, remote, piliferous punctures, which are smaller and closer on the genae and gula, where they bear pale, erect pubescence as opposed to piceous setae on the frons, vertex and occiput ; frons swollen medially above the antennae the swelling roundly bitumescent, concave between the tumescence and the eye-margins ; clypeus polished and shining on the basal half, which has a median, longitudinal tumescent area, most prominent distally, the distal portion of the clypeus subnitent, transversely microstriate, the junction of the two areas sharply defined and bearing a row of small, setiferous punctures, the setae long and sub-erect; ocelli is an isosceles triangle, widest at the base, each ocellus situated on the inner slope of a slight depression, so that their axes are divergent; distance of lateral ocelli from eye-margins 1·6 times their distance from each other; mandibles dark castaneous, piceous beneath and at the base externally, with a well-developed pre-apical tooth and a keel on the face extending from the base to the inner border of the tooth, shining and with elongate, rather deep, setiferous punctures except apically; antennal scape, pedicel and first three flagellar segments ferruginous, fourth flagellar segment somewhat darker, apices of flagellar segments narrowly piceous, fifth to tenth flagellar segments wholly piceous, the whole flagellum with cinereous micropubescence. Eyes glabrous. Relative widths of head, pronotum and second abdominal segment 1·45 : 1 : 1·37.

Thorax bright ferruginous, polished and shining, with scattered, erect, piceous setae dorsally and short, pale pubescence laterally and ventrally; pronotum with a median, longitudinal furrow extending from the anterior margin of the dorsum for about one-half, with remote, feeble punctures dorsally, impunctate laterally, the neck transversely rugulose; proepisternum with fine, moderately close punctures and short, pale pile; scutum of mesothorax convex, slightly darker than the rest of the thorax, with a few scattered punctures and erect, piceous setae; scutellum strongly convex, nearly impunctate; mesopleuron polished and shining, with a few scattered punctures on the anterior half, the posterior portion obliquely striate, spiracle ochreous; propodeon polished and shining, with a few, small, scattered punctures and erect, piceous setae.

Legs.—Coxae ferruginous, clothed with fine, pale pubescence; anterior trochantera piceous, intermediate and posterior trochantera castaneous; femora black above and posteriorly, suffused with castaneous at the base anteriorly and beneath, clothed with sparse, erect, pale pubescence; internal face of posterior femora sinuate; anterior tibiae black, except the extreme base and apex castaneous, calcar luteous; intermediate and posterior tibiae piceous, castaneous at base and apex, calcaria pale, tibial spines fusco-testaceous, sparsely clothed with erect and decumbent, pale pubescence; tarsi fusco-testaceous; claws with a basal tooth.

Abdomen black, except a dark castaneous suffusion on either side of the dorsum of the first tergite, the first sternite, which is ferruginous on the apical half, and the apex of the last segment dark castaneous; the whole abdomen polished and shining, with scattered, remote, shallow punctures and sparse, erect, piceous setae dorsally and laterally; sternites with the punctures tending to a transverse arrangement, clothed with sparse, pale pubescence, more dense on the first and second; last sternite with small, confluent punctures ventrally and laterally.

Holotype.—♀, MALAYA: Selangor, Kuala Sleh (No. 0714), 10.xi. 1946 (*H. T. Pagden*). In author's collection.

Methoca penthesilea* sp. n.

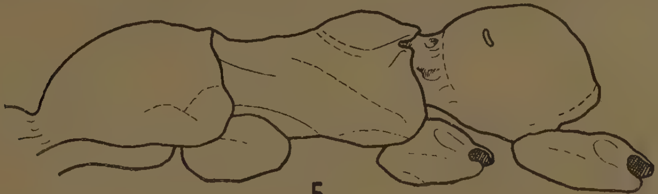
♀. Black, except the antennae and legs more or less, the mandibles, last tergite and last two sternites of the abdomen entirely, ferruginous; clothed with sparse, erect, piceous pubescence and sparse, decumbent, pale, glittering pubescence. Frons above the antennae entirely simple; cheeks strongly receding behind the eyes; clypeus slightly swollen medially, simple, the margin nearly transverse, the surface feebly punctate; ocelli in an isosceles triangle, nearly equilateral, narrowest at the base; mandibles with a strong keel on the face, the keel terminating in a strong, pre-apical tooth on the inner margin. The whole insect polished and shining. Length 5 mm.

Head black, polished and shining, with fine, remote, piliferous punctures on the vertex, occiput and genae, and with a few, scattered, coarser punctures, interspersed with very

---

* Penthesilea, a Queen of the Amazons.

fine punctures, on the frons medially; frons shallowly, transversely concave, strongly receding towards the antennal insertions; median area of clypeus evenly swollen, with fine, close punctures on the distal half, the proximal half glabrous and subnitent medially, the margin very feebly emarginate, almost transverse, the lateral angles rounded, obtuse, the lateral margin receding and feebly emarginate; eyes strongly diverging towards the base of the mandibles, clothed with short, sparse, erect, pale pubescence; ocelli in an isosoceles triangle, nearly equilateral, narrowest at the base, distance of posterior ocelli from the eyes about equal to their distance from each other; mandibles ferruginous, with a strong, acute, pre-apical tooth on their inner margin, the face with a strong keel, extending from the base to the inner margin of the pre-apical tooth; scape piceous, the apex dark ferruginous, dull and micro-punctate beneath; pedicel distinctly ferruginous; base of first flagellar segment ferruginous, the rest of the first, the whole of the second, third and fourth, and the basal half of the fifth, dark castaneous, remaining flagellar segments black; antennae clothed with moderately dense, fine, cinereous pubescence; vertex and frons above clothed with sparse, erect, fuscous pubescence; lower half of inner eye margins with a line of fine, decumbent, silvery pubescence; mandibles with moderate, sub-erect, pale pubescence; genae and head beneath with sparse, sub-erect, silvery pubescence. Relative widths of head, pronotum and second tergite 1·5 : 1·0 : 1·4 (micrometer readings 3·7 : 2·5 : 3·5).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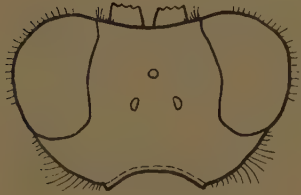
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Figs. 5–6.—(5) Side view of thorax of *Methoca penthesilea* sp. n., ♀; (6) Dorsal view of head, of *M. penthesilea* sp. n., ♀.

Thorax black, polished and shining, clothed dorsally with short, sparse, erect, piceous pubescence, laterally with fine, sub-erect, silvery pubescence; dorsum of thorax with a few, fine, scattered punctures; neck of prothorax finely shagreened anteriorly, with a transverse row of foveae, separated by short costae, posteriorly; anterior constriction of mesothorax medially longitudinally keeled in the anterior two-thirds, with a few foveae along the anterior margin; scutellum distinctly defined, gibbous; anterior constriction of metanotum with a transverse row of foveae, separated by short costae; coxae black, clothed with fine silvery pubescence; trochantera ferruginous; anterior femora black, intermediate and posterior femora piceous above, all the femora ferruginous beneath; anterior tibiae piceous externally, ferruginous on their inner surface, which is densely micropunctate; intermediate and posterior tibiae dark fuscous basally, piceous above and ferruginous beneath, medially and apically; tarsi ferruginous, the claw joint piceous, claws bifid, ferruginous, the tarsi clothed with fine, tawny pubescence; calcaria pale ferruginous.

Abdomen, black, except the last tergite and the last two sternites translucent, clear ferruginous, polished and shining; clothed with very sparse, erect and sub-erect, pale glittering pubescence, that on the sternites tending to form thin, apical fringes; tergites with scattered, very sparse, fine, piliferous punctures, and exceedingly minute, scattered, simple punctures; first sternite dull, finely rugulose on the basal half, the apical half and the remaining sternites polished and shining with minute, sparse punctures, which tend to be closer towards the apical margins, but are nowhere close; punctures on fifth sternite rather more dense and regular; last sternite almost impunctate; sting sheath black, clearly visible through the last segment.

Holotype.—♀, FEDERATED MALAY STATES: Selangor, Serdang, Central Experiment Station of Department of Agriculture, among *Capsicum* in nursery (No. 0422), 13.xii.1937 (*H. T. Pagden*). In author's collection.

After capture the specimen was kept alive for a few days in the hope of being able to breed from it, but no Cicindelid larvae of any species could be found. During its period of captivity it lost the last two segments of the left antenna and the last four segments of the right antenna, also the claws of the left intermediate leg. It is possible that it was attacked by small ants, which gained entry to the cage, and no other explanation of this mutilation seems possible.

Apart from colour, which is not in itself a criterion, this species differs from *violaceipennis* Cameron in the simple clypeus, there being no median tubercle, in lacking tubercles and longitudinal rugulosities on the frons, in having the ocelli comparatively larger and much more widely spaced, and the inner tooth on the mandibles more strongly developed. In the thorax the neck of the prothorax is finely shagreened, not transversely strigose, anteriorly, and there are no tubercles on the mesosternum in front of the intermediate coxae.

MUTILLIDAE.

Timulla Ashmead.

Subgenus *Trogaspidia* Ashmead.

The *erato* Group.

The members of this group are all characterized by the spatulate calcar of the anterior tibiae and by the remarkable form of the clypeus, which has the lateral angles of the median area strongly elevated.

In the males the scutellum is evenly rounded, not at all gibbous, and the hypopygium bears incipient ridges or elongate tubercles.

In the majority of Oriental *Trogaspidia* which have an evenly rounded scutellum the hypopygium is simple, without any sign of tubercles or ridges, so that in this respect the males of the *erato* group are intermediate between those with a gibbous scutellum and hypopygial ridges and those with evenly-rounded scutellum and simple hypopygium.

The female of only one of the six known species has been discovered and is described in this paper.

The distribution of the group, as at present known, is Assam, Burma, Siam, Malaya, Java and Borneo, the species occurring as under :

Timulla (*Trogaspidia*) *stephani* (Magretti), BURMA.
T. (*T.*) *sceva* (Cameron), BURMA and ASSAM.
T. (*T.*) *mickeli* sp. n., SIAM and MALAYA.
T. (*T.*) *erato* Mickel, BORNEO.
T. (*T.*) *selene* sp. n., JAVA.
T. (*T.*) *sondaica* sp. n., JAVA.

Mickel (1935) was the first to point out the peculiar characters of the group when he described *erato*. Magretti described *stephani* in 1892, but, although he remarked on the unusual form of the second abdominal tergite, he made no mention of the other peculiarities referred to above. Bingham (1897, *Fauna of British India*, Hymenoptera **1** : 43 and 44) mentions and figures an insect which has some resemblance to *stephani* under that name, but this is, I think, a specimen of *sceva* (Cameron). The description given by Bingham is a straight translation of Magretti's original description in Latin of *stephani*.

The name *sceva* (Cameron) has for long been a puzzle to me. It does not appear in Dalle Torre, *Catalogus Hymenopterorum* (1897), nor in André, *Genera Insectorum* (1903). A careful search of all Cameron's published papers which were known to me failed to discover a description of this species and, eventually, I described the species, keeping Cameron's name, and selected a holotype from among the material in the British Museum (Natural History) and made the other specimens there, and that in the Rothney collection at Oxford, paratypes. Just before publication of this paper I fortunately discovered Cameron's description of *sceva* (1904, *Zeitschrift für systematisches Hymenopterologie und Dipterologie* **4** : 6). In this paper (*Descriptions of New Genera and Species of Hymenoptera from India*) Cameron states that the type is in the Rothney collection. As Cameron labelled several specimens as type, the specimen in the Rothney collection must now be designated the lectotype.

In this paper I reproduce Cameron's original description and add thereto my own.

Except for *erato* all the species in this group appear to be hill insects.

Key to the species of the *erato* Group.

Males.

1. Scape of antennae with a single distinct carina beneath . . . . . 2.
   Scape of antennae bicarinate beneath . . . . 3.
2. Median area of clypeus with the elevations in the form of a flattened demi-lune, the margin abruptly and deeply notched *selene* sp. n. (p. 200).
   Median area of clypeus with the elevations distinctly convex, but with a small, flattened, lunate area distally, the margin deeply, but not abruptly notched . . . . *erato* Mickel (p. 200).
3. Abdomen with one or more fasciae of pale pubescence . . . . . . 4.
   Abdomen without fasciae ; lateral elevations of median area of clypeus distinctly divergent and truncate distally . . *sondaica* sp. n. (p. 208).

4. Abdomen with two fasciae of golden pubescence, narrowed medially, that on tergite 3 more dense than on tergite 4. Abdominal segments 1–4 with sparse, erect, pale pubescence . . *stephani* (Magretti) (p. 204).
   Abdomen with a single fascia of pale pubescence on tergite 3 . . . . 5.
5. Abdominal segments 1–5 with sparse, erect, pale pubescence; fascia on tergite 3 not dense, interrupted medially . . *sceva* (Cameron) (p. 205).
   Abdominal segments 1–3 with sparse, erect, pale pubescence; fascia on tergite 3 dense, narrowed medially . . . . *mickeli* sp. n. (p. 201).

Timulla (*Trogaspidia*) *erato* Mickel.

Mutilla ira Cameron, 1902, *J. Straits Br. R. Asiat. Soc.* **37** : 74, ♂ (in part).
Timulla (*Trogaspidia*) *erato* Mickel, 1935, *Trans. R. ent. Soc. Lond.* **83** : 241, ♂.

Holotype.—♂ BORNEO: Sandakan (*Baker*). In United States National Museum.

I have not seen the holotype but have examined several paratypes. The species is so far recorded only from British North Borneo and Sarawak.

Timulla (Trogaspidia) selene sp. n.

A species of the *erato* group and closely related to that species from which it differs principally in the clypeus, which has the elevations broadly flattened and punctate, their outer margins acute, the median emargination deep and narrow.

♂. Head, thorax and last four abdominal segments black, first three abdominal segments, except the first sternite, ferruginous, the first sternite largely black; scape with a single distinct carina beneath; first and second flagellar segments subequal; hypopygium with a pair of median, basal, acute tubercles. Wings fuscous, sub-hyaline in the basal third. Length 14 mm.

Head black, sculpture and pubescence as in *erato* Mickel; clypeus as above; scape flattened and widened distally, with a single distinct carina beneath; first and second flagellar segments equal or subequal in length (the first shorter than the second in *erato*); antennal scrobes carinate above. Relative widths of head and thorax, including the tegulae, 1·0 : 1·18 (micrometer readings 5·5 : 6·5).

Thorax exactly as in *erato* except that the pubescence on the mesonotum and scutellum is black or piceous, not at all fuscous.

Abdomen with the first sternite mostly black, otherwise the colouring and pubescence as in *erato*; tergites 3 to 6 with very remote, small punctures dorsally, much more sparse than in *erato*, close punctures laterally; sternites 3–6 with moderately small, sparse punctures, closer laterally; sternite 7 with an acute tubercle near each postero-lateral angle; hypopygium with a pair of median, large, acute, parallel tubercules at the anterior margin (these are slightly convergent in *erato*), the pre-apical tuft of pubescence fuscous.

Wings fuscous, except the basal third sub-hyaline; vein M_2 joining cell R_4 at the middle (at two-thirds in *erato*).

Legs black, with pale pubescence, calcaria pale, anterior calcar spatulate, more expanded than in *erato*; external apical tibial spines four on both intermediate and posterior tibiae, the spines piceous; in *erato* there are five spines on the intermediate tibiae.

The spines referred to are truly apical, there may be sub-apical spines which should not be confused with the apical ones.

Holotype.—♂, WEST JAVA: Djampang, G. Malang, 3000 ft., February. 1935 (*M. E. Walsh*). In Zoölogisch Museum, Buitenzorg, Java.

Paratype.—♂, West Java : Djampang, G. Malang, 3000 ft., February, 1935 (*M. E. Walsh*).

Other specimens examined.—West Java : ♂, Strand Salatri, South Coast, i.1938 (*M. E. Walsh*) ; ♂, Buitenzorg, Tjibarangbang, Mt. Salak, 1200 ft., xi.1937 (*M. E. Walsh*).

I have compared these specimens both with the original description and with a paratype of *erato* Mickel and can find no other differences than those mentioned. The considerable difference in the form of the elevations and margin of the clypeus, the subequal first and second flagellar segments and the venation seem to be sufficient evidence for regarding it as a distinct species rather than a subspecies.

Timulla (Trogaspidia) mickeli sp. n.

Differs from *erato* and *selene* in the bicarinate scape, the pubescence of the third tergite, the form of the tubercles on the hypopygium and in punctuation. There are also differences in the genitalia.

This is the only species in this group of which the female is definitely known.

I have much pleasure in dedicating this species to Professor Clarence E. Mickel, whose critical work on the MUTILLIDAE has done so much towards the advancement of our knowledge of the group.

♂. Head, thorax, legs and last four abdominal segments, black ; first three abdominal segments, except the carina of the first sternite, light ferruginous, the third tergite with a broad, apical fascia, interrupted medially, of dense, appressed, pale pubescence ; median area of clypeus strongly elevated, triangular, deeply concave within, the antero-lateral angles strongly elevated, ovate and glabrous, the anterior margin medially deeply and roundly emarginate ; scape bicarinate beneath ; hypopygium with a pair of glabrous, convergent, lunate tubercles, extending from the base to one-half ; calcaria of anterior tibiae spatulate, finely serrate inwardly towards the extremity, which is spinose ; wings fuscous except at the extreme base. Length 16 mm.

Head black, clothed with sparse, erect, pale golden pubescence, except beneath where it is silvery ; pubescence on frons medially, and along the inner eye-margins, decumbent, pale golden ; clypeus as above, the lateral areas micro-tugulose, dull, clothed with long, decumbent, pale pubescence, the median area clothed at the base and along the sides with dense, sub-erect, pale golden pubescence, the ovate elevations glabrous, polished ; mandibles robust, excised beneath, forming a strong blunt tooth ; face of mandible with a strong carina along the outer margin, the carina confluent with a blunt tooth situated near the apex on the inner margin, the apex simple : face of mandibles concave ; scape bicarinate beneath, irregularly punctate and clothed with sparse, pale golden pubescence on the inner surface ; apex of scape tinged dark ferruginous : second flagellar segment distinctly longer than the first ; ocelli moderate, the lateral ocelli distant about three times their diameter from the eyes ; frons and vertex with coarse, dense, confluent punctures, genae with moderate, confluent punctures, the punctures less deep ; antennal scrobes carinate above. Relative widths of head and thorax, including the tegulae 1·0 : 1·24 (micrometer readings 5·0 : 6·2).

Thorax black, clothed on the pronotum posteriorly, the mesonotum anteriorly, the propodeon and the mesepimeron with sparse, erect, and dense, appressed, golden pubescence ; mesonotum and scutellum anteriorly, with sparse, sub-erect, black pubescence, rest of scutellum and propodeon with long, sparse, erect, and dense, appressed, pale pubescence, not at all golden; pronotum, mesonotum and scutellum coarsely, confluently punctate, the scutellum not gibbous, but with a median, longitudinal, glabrous ridge; propodeon reticulate, with a median, basal area, the posterior half of which is about one-third as wide as the basal half; dorsum and posterior face of propodeon evenly sloped; prepectus micropunctate and micropubescent, the posterior margin with moderately long, pale pubescence; mesepimeron coarsely, confluently punctate, except the anterior concavity micropunctate and micropubescent; mesepisternum coarsely, confluently punctate, micropunctate and microrugulose along the posterior margin; metapleura micropunctate and micropubescent; sides of propodeon reticulate above, micropunctate and micropubescent ventrad; tegulae black, polished and shining, with a few setiferous punctures along the anterior and inner margin.

Abdomen.—Tergites 1–3 pale ferruginous, clothed with sparse, erect, pale pubescence, the first with a very thin apical fringe, the second with a wider, more conspicuous and more dense apical fringe, narrowly interrupted medially, the third with a broad, apical fascia, widely interrupted anteriorly, unbroken posteriorly, of dense, appressed, pale golden pubescence; remaining tergites black, clothed with sparse, erect and sub-erect, black pubescence; first tergite with moderate, confluent punctures, except along the apical margin with a few, fine, separate punctures; second tergite moderately swollen laterally, with a strong, sinuate, transverse ridge, strongly swept back to the lateral swelling, the tergite in profile strongly gibbous on the ridge, the portion anterior to the ridge concave, the anterior area with moderately large, confluent punctures laterally, the punctures small, sparse and separate medially, those below the felt-line small and separate, the posterior area with very sparse, small punctures medially, extreme laterally with moderate, close, confluent punctures, the lateral thirds of the margin with fine, dense, separate punctures; tergites 3–6 with dense, fine, separate punctures on the anterior third, the median third with moderate punctures, close laterally, sparse medially, the posterior third with some moderately fine, scattered punctures beneath the pubescence; the punctures in the anterior third of the sixth tergite less dense than in the preceding tergites; the surface between the punctures on the anterior third of all these tergites very finely, transversely tessellated; last tergite with fine, close, separate punctures at the extreme base, the remainder, except the glabrous, tumescent, area, with moderately small, dense, confluent punctures; tumescent area long, narrow anteriorly, evenly widening posteriorly, where it is three-fifths as wide as the margin of the segment; first sternite ferruginous, the carina black, with sparse, erect, pale pubescence; second and third sternites ferruginous, clothed with sparse, erect, pale pubescence, and with a thin apical fringe of pale golden pubescence; remaining sternites black, with black pubescence; first sternite with a few foveolate punctures; second sternite with an anterior, median gibbosity, with moderately large, separate punctures, sparse medially, finer and denser postero-laterally, with an ovate area, entirely free from punctures and pubescence, covering the extreme lateral half; third to sixth sternites with moderately small, sparse punctures, remote medially, dense in the postero-lateral angles; seventh sternite with moderately small, scattered punctures, and with an acute, triangular tubercle at about one-half, situated extreme laterally and directed inwards; hypopygium with a pair of glabrous, lunate, convergent tubercles, extending from the base to one half, the lateral margins carinate, the surface with small, moderately close punctures.

Legs black, clothed with pale pubescence; calcaria pale.

Wings fuscous, except the extreme base pale; cell 2nd $R_1 + R_2$ angulately truncate at the apex, about equal in length to cell R + 1st R_1; cell R_4 not at all obsolete.

♀. Head and abdomen black; thorax, scape, coxae, trochanters, most of the femora, anterior tibiae externally and first sternite, ferruginous; second tergite with a pair of anterior spots of pale golden pubescence, separated by a distance about one and one-sixth times their greatest diameter, the apical margin of the tergite with a narrow fringe of pale golden pubescence; third tergite clothed with dense, appressed, pale golden pubescence, narrowly interrupted anteriorly with black; remaining segments black; pygidial fringes pale golden ; pygidial area finely, longitudinally rugulose on the basal two-thirds, almost striate. Length 9·5 mm.

Head black, clothed with sparse, erect, black pubescence and sparse, sub-erect, pale pubescence on the frons and vertex, the vertex posteriorly with dense, erect, fuscous pile ; genae and post-genae with erect and sub-appressed, pale pubescence ; margin of clypeus strongly bidentate, widely emarginate between the denticles ; median area of clypeus narrowly triangular, raised, bearing a strong, median, downwardly directed, sharp, submarginal tubercle ; mandibles castaneous, black at base and apex, the apex simple ; antennal scrobes piceous, finely pubescent ; scape ferruginous, with a few, shallow punctures and sparse, pale golden pubescence ; pedicel and flagellum black, the first flagellar segment nearly as long as the second and third together ; antennal scrobes carinate above ; genae carinate posteriorly from the mandibular articulation to about one-third of the way to the vertex ; gular carina produced into a moderately strong tooth on either side of the mouth cavity ; frons and vertex moderately coarsely, confluently punctate, the genae less coarsely so. Relative widths of head and thorax at its widest part 1·06 : 1·0 (micrometer readings 9·0 : 8·5).

Thorax ferruginous, moderately coarsely, confluently punctate on the dorsum, the sculpture with a longitudinal trend on the mesonotal area ; clothed with sparse, erect and sparse, decumbent, dark ferruginous pubescence ; scutellar scale well developed, rather more than one-sixth the width of the thorax at that part ; thorax steeply, but smoothly, rounded into the propodeon ; posterior face of propodeon longitudinally rugose, the anterior face somewhat denticulate, the posterior face clothed with sparse, erect, pale pubescence ; humeral angles moderately prominent, the pronotum widened posteriorly to the angles, forming a prominent, obtuse, denticle ; mesonotum slightly narrowed posteriorly, laterally sinuate ; sides of propodeon feebly denticulate ; lateral margins of thorax dark ferruginous, almost piceous, sub-carinate ; pronotum laterally with the anterior margin feebly, but distinctly, carinate, finely pubescent along the anterior margin and in the concavity, with a strong, prominent carina arising from the humeral angle and extending to the postero-ventral angle, the triangular, dorsal area thus formed micropubescent and with a few, fine, scattered punctures ; mesopleura micropubescent, the anterior area micro-shagreened, the posterior area micropunctate ; metapleura and sides of propodeon micropubescent and micropunctate.

Abdomen black, with sparse, erect and sub-erect, black pubescence on tergites 2, 4 and 5 ; first tergite with sparse, erect, pale pubescence and moderate, confluent punctures ; second tergite with close, moderate punctures, smaller and sparser medially, with some sparse, erect, pale pubescence anteriorly and with a pair of anterior, subcircular spots of appressed, pale golden pubescence, the spots somewhat elongate and separated by a distance about one and one-sixth times their greatest diameter, the tergite slightly flattened between the spots ; apical margin of second tergite with a narrow fringe of pale golden pubescence ; third tergite clothed with dense, appressed, pale golden pubescence, narrowly excised anteriorly in the middle ; fourth and fifth tergites with fine, dense punctures anteriorly, clothed with moderately dense, sub-appressed and sparse, erect, black pubescence on the posterior two-thirds ; last tergite with fine, dense punctures laterally, pygidial fringes pale golden, pygidial area well defined, finely, longitudinally rugulose on the basal two-thirds, the apex smooth ; first sternite dark ferruginous, the carina pale ferruginous and translucent, its angles rounded ; second sternite with moderately large, moderately dense, almost confluent punctures, except in the anterior lateral thirds on either side of the median, longitudinal carina with the punctures smaller and separate, clothed with sparse, erect, pale pubescence and with a thin apical fringe of pale golden pubescence ; third to fifth sternites with moderately fine, dense punctures, sparse, erect, pale pubescence and a thin, apical fringe of pale golden pubescence ; last sternite with moderately fine, dense punctures and sparse, erect, pale pubescence.

Legs.—Anterior legs ferruginous, except the tibiae posteriorly and the tarsi, piceous ; intermediate and posterior legs with the coxae, trochanters and femora, except their extreme apex, ferruginous, apex of femora dark fuscous, tibiae and tarsi black; all the legs clothed with pale pubescence, that on the tarsi distinctly, on the tibiae faintly, golden; calcaria pale golden.

Holotype.—♂. FEDERATED MALAY STATES: Pahang, Fraser's Hill, Peninjau, 4200 ft., 2.vi.1936 (*H. M. Pendlebury*), *in copula* with ♀ allotype. In Selangor Museum, Kuala Lumpur, F.M.S.

Allotype.—♀. FEDERATED MALAY STATES: Pahang, Fraser's Hill, Peninjau, 4200 ft., 2.vi.1936 (*H. M. Pendlebury*), *in copula* with ♂ holotype. In Selangor Museum, Kuala Lumpur, F.M.S.

Paratypes: FEDERATED MALAY STATES: ♀, Selangor, Bukit Kutu, 3500 ft., 30.i.1930 (*H. T. Pagden*); ♀, Pahang, Fraser's Hill, 4200 ft., 18.vi.1931 (*H. M. Pendlebury*); ♂, Pahang, Fraser's Hill, 4200 ft., 6.vii.1931 (*H. M. Pendlebury*); ♂, Pahang, Fraser's Hill, 4000 ft. 28.vi.1933 (*H. M. Pendlebury*); ♂, Pahang, Fraser's Hill, 4000 ft., 1.vii.1933 (*H. M. Pendlebury*); ♂, Selangor, Bukit Kutu, 3400 ft., August, 1935 (*H. M. Pendlebury*); 7 ♂, Pahang, Fraser's Hill, 4200 ft., 14, 15, 17, 18, 19 (2), and 21.vii.1936 (*H. M. Pendlebury*).

UNFEDERATED MALAY STATES: ♂, Kedah, Kedah Peak (Gunong Jerai), 3000–3300 ft., 12.iii.1928 (*H. M. Pendlebury*).

SIAM: ♂, Nakon Sri Tamarat (Nagorn Sridharmraj) Khao Luang, 3000 ft., 30.iii.1922 (*H. M. Pendlebury*).

Timulla (*Trogaspidia*) *stephani* (Magretti).

Mutilla stephani Magretti, 1892, *Ann. Mus. civ. Stor. nat. Genova* (2) **12**: 227, ♂.
Mutilla stephani Bingham, 1897, *Fauna Brit. India*, Hym. **1**: 43, ♂.
Mutilla stephani Dalla Torre, 1897, *Cat. Hymen.* **8**: 88, ♂.

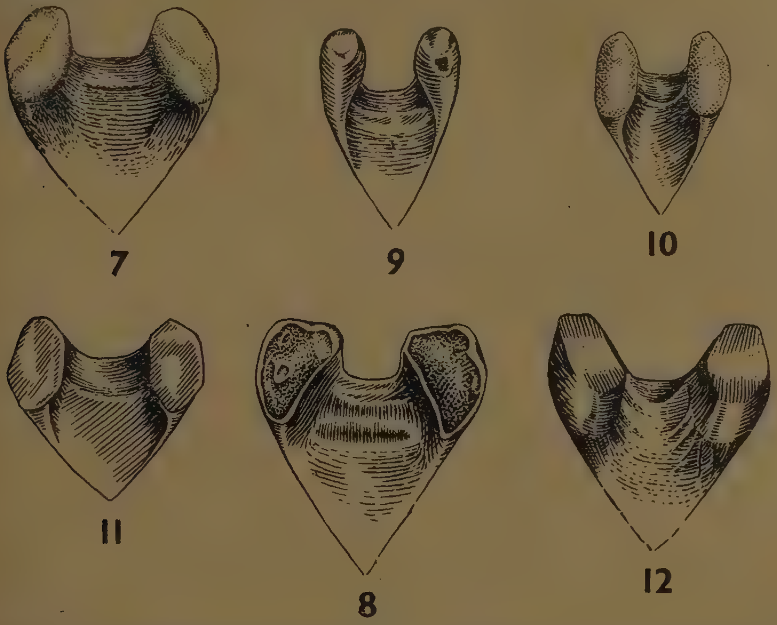
The original description of this species, although it makes no mention of the spatulate anterior calcar nor of the peculiar form of the clypeus, states that the second abdominal tergite bears a prominent, transversely compressed gibbosity. This fact, together with the general facies, as visualized from the description, led me to believe that it might belong to the *erato* group. Through the good offices of Mr. R. B. Benson of the British Museum (Natural History) and the kindness of Professor Oscar de Beaux, Director of the Museo Civico di Storia Naturale, "Giacomo Doria," Genoa, who sent the type material to Mr. Benson for me to examine, I have been able to confirm my suspicions. The material submitted was complex, and I hope to deal with the other species represented at a later date, but the type specimen was clearly indicated so that there can be no doubt of its identity.

The differences between *stephani* and *mickeli* are not great, but I think that they are sufficient to justify considering them as specifically distinct and not merely subspecies. The most obvious difference lies in the pubescent fasciae of the abdomen, *stephani* having an apical fascia on both tergites three and four, that on three of dense, appressed, golden pubescence, widely emarginate medially on the anterior border, that on four of sub-appressed, golden pubescence, narrower, widely emarginate on the anterior margin medially, while *mickeli* has but a single abdominal fascia of appressed, very pale golden pubescence on the third tergite.

Other differences are:

Head slightly more pubescent, genae with finer and shallower punctures, median emargination of clypeus slightly less wide relative to the width across the tubercles (0·75 : 2·75 as compared with 1·0 : 2·75 for *mickeli*). Length of median area of clypeus measured from the margin, relative to width at base of tubercles slightly less than in *mickeli*. Relative widths of head and thorax, including tegulae 1·0 : 1·16 (micrometer reading 5·0 : 5·8) in *stephani*, 1·0 : 1·24 (micrometer reading 5·0 : 6·2) in *mickeli*.

Thorax with the line of appressed golden pubescence along the anterior margin of the mesonotum very narrow, much narrower than in *mickeli* ; scutellum with only a feeble indication of a longitudinal, median, glabrous ridge.



FIGS. 7–12.—(7)[1] Median area, clypeus of : *T.* (*T.*) *erato* Mickel, ♂ ; (8) *T.* (*T.*) *selene* sp. n. ♂ ; (9) *T.* (*T.*) *mickeli* sp. n., ♂ ; (10) *T.* (*T.*) *stephani* (Magretti), ♂ ; (11) *T.* (*T.*) *sceva* (Cameron), ♂ ; (12) *T.* (*T.*) *sondaica* sp. n., ♂.

Abdomen with sparse, black pubescence only on tergites 5–7 ; punctures on second tergite finer and less dense laterally, both in the anterior and posterior areas ; first sternite more extensively black basally ; fourth and fifth sternites with sparse, erect, pale pubescence and with a thin, apical fringe of pale golden pubescence.

Type.—♂, BURMA : Karen Hills, 900–1000 m., June–August, 1888. In Museo Civico di Storia Naturale, Genoa, Italy.

Timulla (*Trogaspidia*) *sceva* (Cameron).

Mutilla sceva Cameron, 1904, *Z. Hymen. Dipt.* 4 (1) : 6, ♂.

This species, like *stephani*, occurs in Burma, but extends Northwards into Assam. It is dealt with here because it falls naturally into the *erato* group, and its inclusion completes the list of known species of that group.

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[1] See footnote, p. 217.

Timulla (*Trogaspidia*) *sceva* was described as *Mutilla sceva* by Cameron in 1904 in a paper dealing with Indian Hymenoptera.

Four specimens are known to me, all males, and three bear labels " *Mutilla sceva* " in Cameron's handwriting. One of these specimens is in the Rothney collection, Hope Department of Zoology, Oxford University, and two specimens are in the British Museum (Natural History), South Kensington. All these specimens are labelled "Type." The fourth specimen was assigned by Bingham to *stephani* (Magretti).

Cameron gives the location of the type as " Coll. Rothney," and I therefore designate the specimen in that collection as the lectotype.

Timulla (*Trogaspidia*) *sceva* (Cameron).

Lectotype.—♂. ASSAM: Khasi Hills. In Rothney collection, Hope Department of Zoology, Oxford University.

Cameron's original description follows :

> " Black ; the apex of the 1st and the whole of the 2nd and 3rd segments ferruginous ; the basal half of the end segment with an oblique slope ; the wings fusco-violaceous, paler at the base ; the apex of the clypeus stoutly bidentate. Length 15–16 mm.
>
> " Hab. Khasi Hills. (Coll. Rothney.)
>
> " Antennae black, the scape covered with long white hair. Head thickly covered with long grey hair ; the front and vertex rugosely punctured. Clypeus smooth, bare and shining ; the middle deeply depressed ; the apex ending in two broad teeth ; their apex is bluntly rounded. Pro- and mesonotum rugosely punctured ; the base of the propleurae coarsely punctured, the apex smooth. The central part of the mesopleurae closely, but not very strongly, punctured. The apex of the pronotum thickly covered with griseous pubescence ; the mesopleurae in the middle covered with a silvery pile and more sparsely with long white hair. Mesonotum thickly covered with fuscous hair ; its furrows are clearly defined. Scutellum roundly convex, but not much raised ; rugosely punctured ; its centre at the base smooth ; its sides and apex covered with long blackish and pale hair. Median segment reticulated ; the base of the pleurae smooth ; it has a gradually rounded slope to the apex ; the central basal area is small, irregular and not clearly defined. Legs black, thickly covered with griseous hair ; the calcaria pale, the tarsal spines rufous. Wings fusco-violaceous, paler at the base ; the stigma and nervures black ; there is an oblique hyaline cloud in the 1st cubital cellule. Abdomen black ; the apex of the petiole and the whole of the 2nd and 3rd segments ferruginous ; the 1st segment is coarsely punctured except at the apex ; the ventral keel is slightly dilated at the base ; the 2nd segment, on the basal half, is olbiquely depressed and is there closely, but not strongly, punctured ; the apex is smooth. The middle segments are fringed with white hair ; the apical more thickly with longer black. The last segment is coarsely punctured, except in the middle, where there is a smooth band, which becomes wider towards the apex. The apex of the last ventral segment is smooth and bare ; the rest covered with long black hair ; at the base of the smooth part are 2 rounded tubercles.
>
> " Characteristic of this species is the incised bidentate clypeus. The mandibles end in one, distinctly separated, tooth. The only Indian species of *Mutilla* with a bidentate clypeus is *M. bidens* Cam. (*Ann. and Mag. of Nat. Hist.*, July, 1899), but that species is smaller, the mesonotum is not furrowed, the scutellum furrowed and the last ventral segment bears two keels."

To this description I add the following more detailed remarks :

♂. Head, thorax and last four abdominal segments black ; first sternite and base of first tergite piceous ; second and third abdominal segments ferruginous ; third tergite with a distinct, but not dense, medially interrupted fascia of pale golden pubescence; scape bicarinate beneath; second flagellar segment slightly longer than the first, but not noticeably so; hypopygium with a pair of median, basal, blunt tubercles, acute when viewed laterally, nearly parallel and polished externally; wings fuscous, somewhat paler basally, particularly the hind wings. Length (H. + Th.) + Abd. = 8 + 9·05 mm.

Head black, sculpture and pubescence very similar to *erato* Mickel, but the sculpture rather more coarse; clypeus very similar to *erato* with a slight tendency towards *mickeli*, the lateral lunate areas scarcely at all convergent, the median, marginal excision about as in *erato*, relatively less deep than in *mickeli*; scape somewhat flattened, scarcely constricted medially, slightly widened apically, distinctly bicarinate beneath, clothed with sparse, moderately long, sub-erect, pale pubescence; first and second flagellar segments subequal, the second a shade longer than the first; antennal scrobes carinate above; posterior ocelli situated about two and one-third times as far from the eyes as from each other (3·5 : 1·5). Relative widths of head and thorax, including the tegulae, 1·0 : 1·29 (micrometer reading 5·0 : 6·45).

Thorax black, sculpture almost exactly as in *erato* except that the reticulations of the dorsal face of the propodeon are very much larger; pubescence of pronotum rather more dense than in *erato*; dorsum of propodeon moderately densely clothed with sub-appressed, pale, glittering pubescence, the median areolus fusiform, about four times as long as wide.

Abdomen with the first tergite very dark ferruginous to piceous on the basal half, the apical half ferruginous; second and third tergites wholly ferruginous, the remainder black; first tergite with moderate to coarse, confluent punctures, finer posteriorly, clothed with sparse, erect, pale pubescence; second tergite with a transverse, angulate, low ridge, as in the other members of the group, the area anterior to the ridge with moderately coarse, close punctures, scarcely less close medially, the posterior area with small, remote punctures, closer laterally, clothed with sparse, erect, pale pubescence; third tergite with moderate, close, separate punctures, more widely separated medially, clothed with sparse, erect, pale pubescence and with a distinct, but not dense, medially interrupted, apical fascia of sub-appressed, pale, glittering pubescence; fourth to sixth tergites black, with fine, close, separate punctures basally, coarser punctures medially and fine, remote punctures apically; the fourth and fifth with sparse, erect, pale pubescence and a thin apical fringe of pale pubescence, the sixth with sparse, erect, black pubescence; last tergite with fine, close, separate punctures at the base, the remainder, except the median tumescent area, with moderate, close, confluent punctures, clothed with sparse, erect and sub-erect, black pubescence: first sternite piceous, the carina on the anterior two-thirds elevated anteriorly, the lateral areas with a few longitudinal rugae and moderate, irregular punctures, clothed with sparse, erect, pale pubescence, the posterior face with a fine, short, pale pile; second sternite with an anterior, median gibbosity, the anterior third receding and impunctate on the lateral areas, the remainder with moderate punctures separated by about their own diameter, except a small, lateral, ovate area polished and impunctate, clothed with sparse, erect, pale pubescence and with a thin apical fringe of pale pubescence; third sternite ferruginous, with small, close punctures, dense laterally, more remote medially, sparse, erect, pale pubescence and a thin, apical fringe of pale pubescence; fourth to sixth sternites black, with similar puncturation to the preceding sternite, fourth and fifth with sparse, erect, pale pubescence and a thin, apical fringe of pale pubescence, sixth with sparse, erect, fuscous pubescence and a thin, apical fringe of black pubescence; seventh sternite black, with sparse, moderately small punctures and sparse, erect, black pubescence, armed with a prominent, extreme lateral, acute tubercle at about one-half from the apex; hypopygium with a pair of polished, lunate tubercles on the median third basally, the tubercles separated by a distance equal to their distance from the lateral margin; lateral areas of hypogodium with a few, small, shallow punctures, the apical third membranous, clothed with sparse, erect, fuscous pubescence.

Legs black, clothed with pale pubescence; anterior calcaria spatulate, pale, the external convexity castaneous apically ; the other calcaria pale ; external tibial spines of hind legs pale.

Wings fuscous, except the extreme base pale ; cell 2nd $R_1 + R_2$ somewhat truncate at the apex, not distinctly angulate, about equal in length to cell R + 1st R_1 ; cell R_4 not at all obsolete.

Other specimens examined : 2 ♂, ASSAM : Khasi Hills, in British Museum (Natural History), South Kensington ; ♂, Burma, Pegu Hills, viii.1888, Bingham, in British Museum (Natural History), South Kensington (originally attributed to *stephani* (Magr.)).

Timulla (Trogaspidia) sondaica sp. n.

♂. Differs from *erato* Mickel in the distinctly bicarinate scape, in the presence of a distinct, but narrow, medially interrupted, apical fascia of pale pubescence on tergite three, and in the structure of the hypopygium.

From *mickeli* it differs in the puncturation of the abdomen, which is very similar to that of *erato*, in the general colour of the pubescence, particularly in the pale pubescence of tergites four and five, and in the structure of the hypopygium.

Head, thorax and last four abdominal segments, black ; first three abdominal segments ferruginous, except the extreme base of the first tergite and most of the first sternite, black ; legs black, calcaria pale, intermediate tibiae with three, posterior tibiae with four, distinct, dark spines externally at the apex, these spines are pale in *mickeli*, dark in *erato*, where they number five on the intermediate tibiae. Length 16 mm.

Head black, clothed with sparse, erect, pale pubescence on the upper frons, vertex genae and posteriorly, with sub-appressed pale pubescence between the antennal tubercles and on the lower frons, and with longer, sub-appressed and more dense, silvery pubescence along the lower eye-margins inwardly, malar space and clypeus ; mandibles black, with a dark ferruginous pre-apical spot, robust, with a strong, blunt tooth near the base beneath, apex simple, with a single pre-apical tooth on the inner margin ; antennae black, scape bicarinate beneath, clothed with sparse, pale pubescence ; first flagellar segment equal in length to the second ; clypeus as described for *mickeli*, the face of the elevated tubercles ferruginous ; puncturation as in *mickeli*. Relative widths of head and thorax, including the tegulae, 1·0 : 1·25 (micrometer reading 5·0 : 6·25).

Thorax black ; the pronotum with moderately dense, sub-appressed, pale pubescence posteriorly, with sparse, erect, pale pubescence anteriorly, moderately coarsely, confluently punctate ; mesonotum moderately coarsely, confluently punctate, clothed with sparse, sub-erect, black pubescence, except extreme anteriorly with sub-erect, pale pubescence ; scutellum slightly elevated but not gibbous, with a median, longitudinal, glabrous ridge, clothed with sparse, erect, curved, pale pubescence and with a few black hairs anteriorly ; propodeon evenly sloped, the basal area clothed with sub-appressed, not very dense, pale pubescence, the surface reticulate, with a median, elongate, basal area ; sides of pronotum finely pubescent ; mesepimeron with dense, sub-appressed, pale pubescence on the convexity, the pubescence slightly tawny, with moderate, close, confluent punctures, aciculate and micropubescent in the anterior concavity ; mesepisternum with dense, sub-appressed, pale pubescence and moderate, confluent punctures on the convexity, the posterior concavity micropubescent, finely aciculate and with a few, small, scattered punctures ; metapleura micropubescent and finely aciculate ; sides of propodeon shallowly reticulate, except along the metapleural suture, where it is micropunctate and micropubescent ; tegulae black, shining, microscopically tesselated on the posterior half externally, with a few punctures on the anterior and inner margin.

Abdomen.—First to third tergites ferruginous, the first black at the extreme base ; remaining tergites black ; first five tergites with sparse, erect, pale pubescence, the third with a thin, but distinct, medially interrupted, apical fascia of sub-appressed, pale pubescence; first sternite black, second and third ferruginous, remainder black, clothed with sparse, erect, pale pubescence, except the last two segments with black pubescence; first tergite with moderate, confluent punctures, except apically the punctures very fine and sparse; second tergite swollen laterally, with a transverse, sinuate, low ridge from the posterior margin of the lateral swelling curving forwards over the dorsum at one-half, the anterior area in profile feebly concave, almost straight, with sparse, small punctures dorsally, closer laterally, larger and moderately dense on the lateral swelling, the posterior area with very sparse, very small punctures dorsally, almost impunctate, and moderately small, close punctures extreme laterally, clothed with sparse, erect, pale pubescence and with a thin apical fringe of pale pubescence; third tergite with fine, close punctures basally, the surface between the punctures microtesselated, and fine, sparse punctures on the dorsum medially, the punctures closer and slightly larger laterally, clothed with sparse, erect, pale pubescence, and with an apical fascia of sub-appressed, pale pubescence, narrowing towards the dorsum, where it is widely interrupted, the interruption with a few, pale hairs; fourth to sixth tergites black, with fine, dense punctures extreme basally, very sparse, fine punctures medially on the dorsum, the apical margin impunctate; last tergite with the apical margin strongly sinuate, roundly produced medially, the tumescent area strongly widened from base to apex, with small, close punctures laterally; first sternite with a moderately well developed carina, its anterior angle slightly elevated, with a few foveolate punctures laterally; second sternite with moderately small, remote punctures basally, the punctures larger medially, finer along the posterior margin, feebly swollen postero-laterally and with a glabrous, impunctate area on the swelling; third to sixth sternites with fine, remote punctures, denser laterally; seventh with a few, small, scattered punctures and an extreme lateral, blunt denticle at about one-half; sternites 3–5 with a thin apical fringe of pale pubescence, 6 and 7 with sparse, black pubescence; hypopygium with a strong, median, trifid tumescence, the lateral margins divergent, glabrous and sub-tuberculate externally, the median portion rounded posteriorly, extending slightly beyond the lateral arms, the tumescence irregularly punctate, clothed with sparse, black pubescence laterally, more dense, fulvous pubescence at the apex of the tumescence.

Wings fuscous, except the basal third pale; cell 2nd $R_1 + R_2$ angulately truncate apically, longer than cell R + 1st R_1; cell R_5 receiving veins $M_3 + {}_4$ slightly beyond the middle; cell R_4 distinct, except for vein $M_1 + R_{4+5}$.

Legs black, with pale pubescence, calcaria pale; anterior tibial spur spatulate, pale translucent ochreous, with a large, dark spot on the expansion medially; external tibial spines dark.

Holotype.—♂, West Java: Soekaboemi, Sitoegoenoeng, 1000 m., 23.ix.1934 (*J. van der Vecht*). In Zoölogisch Museum, Buitenzorg, Java.

Paratypes: West Java: ♂, Soekaboemi, Sitoegoenoeng, 1000 m., 23.ix.1934 (*J. van der Vecht*); ♂, Djampang Tengah, G. Tjisoeroe, 600–800 m., xi.1933 (*M. E. Walsh*); ♂, Djampang Tengah, G. Tjisoeroe, 600–800 m., iii.1935 (*M. E. Walsh*); ♂, Poentjak, 1400 m., iii.1936 (*E. Jacobson*).

Middle Java: ♂, Dieng, 2060 m., vii.1935 (*E. Jacobson*).

Other specimens examined: West Java: ♂, Mts. Djampang Wetan, Goenoeng Malang, 1000 ft., viii.1937 (*M. E. Walsh*); 3 ♂, Goenoeng Malang, viii.1937 (*M. E. Walsh*); ♂, Mt. Gede, Lebok Siol, 3000–4000 ft., viii.1937 (*M. E. Walsh*); ♂, Balekambang, Tjileboek baai, viii.1937 (*M. E. Walsh*).

The Subspecies of *Timulla* (*Trogaspidia*) *philippinensis* (Smith).

To this group belong some of the largest, if not the largest, members of the *Timulla* subgenus *Trogaspidia* found in the Malay Archipelago. The diagnostic features may be given as follows.

Males: Scutellum gibbous. Hypopygium with elevated, elongate, lateral ridges or tubercles. Mandibles not excised beneath. Second abdominal sternite evenly convex.

Females: Second abdominal tergite with a pair of pale, pubescent spots; third tergite with a fascia of dense, appressed, pale pubescence, interrupted medially or not; pygidial area rugulose. Thorax entirely ferruginous.

The median ocellus in the male is situated in a slight depression, surrounded by a distinct ridge, but this character is not peculiar to the group. The genitalia of all the subspecies of which the male is known are similar, any variation which does occur being mainly in the presence or absence of a denticle on the inner margin of the uncus of the sagitta, but this is not constant so cannot be considered even of subspecific importance.

In the females the sculpture is very constant in all the known subspecies, but there are marked differences in the pale pubescent markings and slight differences in the development of the scutellar scale, in the colour of the legs and in the sculpture of the pygidial area. This last is always more or less rugulose, but the extent of the rugulosity and the disposition of the rugae vary slightly, though they appear to be constant in any one subspecies. The pale pubescent spots of the second tergite may be longitudinally elongate, subcircular or subtriangular. The third tergite always has a dense fascia of appressed, pale pubescence, which may be interrupted. The fourth tergite may be wholly black or may bear a pair of large, subquadrate spots of appressed pale pubescence.

On the whole the females are more difficult to separate than are the males, and the key which I present may not be entirely satisfactory when more subspecies are known. The various subspecies seem to be confined within comparatively narrow geographical limits and the locality is, in many cases, a distinct aid to identification.

In the key to females I have included subspecies *singapora* Mickel, and I have mentioned a unique specimen, which I believe to be this subspecies, in the text. The identity of this specimen is by no means certain, so I have queried it and have not described it. The reason for the tentative indication of the identity of this female is based on the following facts: three subspecies of *philippinensis* have been described from the Malay Peninsula, *malayana* (Cameron) ♂, *skeati* (Cameron) ♀, and *singapora* Mickel ♂. None of these has ever been taken *in copula*, but *malayana* has only been taken on the Eastern side of the Peninsula and the same applies to *skeati*, which is likely to prove the female of *malayana*; *singapora* is only recorded from Singapore Island and from Kuala Lumpur, the latter on the West of the main range of mountains. The female which I have tentatively assigned to *singapora* was taken in Singapore Island and is quite distinct from *skeati*.

The keys which follow are based on those of Mickel (1935), to whom I am deeply indebted for permission to make use of them.

Key to the Subspecies of *Timulla* (*Trogaspidia*) *philippinensis* (Smith).

Males.

1. Pronotum clothed with sparse, black pubescence . . . . 2.
   Pronotum clothed with appressed, pale pubescence . . . . 4.
2. Abdomen with at least segments 2–4 ferruginous or partly ferruginous 3.
   Abdomen entirely black . . . . . *philippinensis itambusa* (Cockerell).

3. Abdominal segments 2–5 ferruginous *philippinensis philippinensis* (Smith) (p. 212).
Abdominal segments 2 and 3 wholly, 4 partly, ferruginous *philippinensis paloeana* subsp. n. (p. 215).
4. Dorsum of propodeon with dense, even, appressed, pale pubescence *philippinensis malayana* (Cameron) (p. 212).
Dorsum of propodeon with only moderately dense, sub-appressed, pale pubescence . . . . 5.
5. Median ridge of clypeus weak, abdominal segments 2–6 ferruginous . 6.
Median ridge of clypeus strong, forming a prominent, dull carina ; abdominal segments 2–4 ferruginous *philippinensis singapora* Mickel (p. 212).
6. Disc of second tergite with distinct, sparse punctures ; apical fringe of sixth tergite ferruginous . . . *philippinensis amartana* (Zavattari).
Disc of second tergite almost entirely glabrous, impunctate ; apical fringe of sixth tergite usually black . . . . 7.
7. Ferruginous pubescence of tergites 2–6 very bright *philippinensis sunda* Mickel (p. 213).
Ferruginous pubescence of tergites 2–6 very dark or black *philippinensis kangeana* subsp. n. (p. 214).

Females.

1. Pale pubescent fascia of third tergite distinctly interrupted medially with black ; fourth tergite with a pair of transverse, pale, pubescent spots . . . . 2.
Pale pubescent fascia of third tergite usually entire, sometimes weakly emarginate with black medially ; fourth tergite either black or with a pair of transverse, pale, pubescent spots . . . . 4.
2. Pubescent markings of abdomen pale golden, almost silvery ; pale pubescence of legs sparse . . . . 3.
Pubescent markings of abdomen strongly golden ; pale pubescence of legs golden, dense . . . . *philippinensis paloeana* subsp. n. (p. 215).
3. Pale spots on fourth tergite separated by a distance about equal to their transverse diameter ; pale pubescence of first tergite entirely erect ; pale hairs of antero-lateral areas of second tergite few, entirely erect, inconspicuous ; scutellar scale distinct *philippinensis sunda* Mickel (p. 213).
Pale spots on fourth tergite widely separated ; pale pubescence of first tergite in part appressed ; pale hairs on antero-lateral areas of second tergite in part appressed, obvious ; scutellar scale weak *philippinensis kangeana* subsp. n. (p. 214).
4. Fourth tergite without a pale fascia or pale pubescent spots . . . 5.
Fourth tergite with pale pubescent spots or with an interrupted pale fascia . . . . 6.
5. Spots on second tergite elongate-ovate, silvery ; carina on first sternite entire . . . . *philippinensis philippinensis* (Smith) (p. 212).
5. Spots on second tergite subtriangular, pale golden ; carina of first sternite weakly emarginate . ? *philippinensis singapora* Mickel (p. 212).
6. Legs entirely black . . . . 7.
Femora more or less ferruginous . . . . 8.
7. Pale spots of second tergite elongate-ovate, large ; pale pubescent spots of fourth tergite small, not broader than long, separated by about twice their transverse diameter . . . *philippinensis williamsi* Mickel.

Pale pubescent spots of second tergite subcircular, small; pale pubescent spots of fourth tergite large, distinctly broader than long, separated by a space slightly greater than their transverse diameter *philippinensis sumbana* subsp. n. (p. 216).

8. Femora ferruginous, except their apices black; fourth tergite with a broad fascia of pale pubescence, interrupted medially with black *philippinensis skeati* (Cameron) (p. 212).

Proximal two-thirds of anterior femora ferruginous, the proximal half of the middle and hind femora usually distinctly ferruginous; fourth tergite with a pair of lateral, transverse spots of pale pubescence, not extending to the lateral margins . *philippinensis amartana* (Zavattari).

Timulla (*Trogaspidia*) *philippinensis philippinensis* (Smith), 1855.

The full synonymy of this subspecies is given by Mickel in 1935, *Trans. R. ent. Soc. Lond.* **83**: 228.

This species has been fully dealt with by Mickel, and further records would merely occupy space to no purpose.

Timulla (*Trogaspidia*) *philippinensis singapora* Mickel.

Timulla (*Trogaspidia*) *philippinensis singapora* Mickel, 1935. *Trans. R. ent. Soc. Lond.* **83**: 229, ♂.

Holotype.—♂, Malaya: Singapore, Straits Settlements (*Baker*). In United States National Museum.

♂, Federated Malay States: Kuala Lumpur, 22.iv.1928 (*H. T. Pagden*), caught on window of laboratory. This specimen has been submitted to Professor Mickel for confirmation.

? ♀, Straits Settlements: Singapore, Bukit Timah, 3.viii.1912. In Selangor Museum, Kuala Lumpur, F.M.S. ? ♀, Straits Settlements, Singapore, MacRitchie Reservoir, i.1947 (*M. W. F. Tweedie*).

There is no definite biological evidence for associating the sexes of this subspecies and only the single female is at present known to me. On the evidence of locality and the fact that only one other subspecies of female, *skeati* (Cameron), which is probably the female of *malayana* (Cameron), is known from Malaya, I think that the association is probably correct. Until there is more definite evidence, however, I refrain from creating an allotype and merely indicate the diagnostic features of the specimen in the key.

Timulla (*Trogaspidia*) *philippinensis malayana* (Cameron).

Mutilla malayana Cameron, 1901, *Proc. zool. Soc. Lond.* **1901**: 16, ♂.
Mutilla malayana André, 1903, *Gen. Insect.* **11**: 71, ♂.
Timulla (*Trogaspidia*) *philippinensis malayana* Mickel, 1933, *Ann. ent. Soc. Amer.* **26**: 395, ♂ (*nec* ♀).
Timulla (*Trogaspidia*) *philippinensis malayana* Mickel, 1935, *Trans. R. ent. Soc. Lond.* **83**: 230, ♂.

Holotype.—♂, Malay Peninsula; Bukit Besar, Jalor (District of Patani State), in British Museum (Natural History).

Distribution.—East Coast of South Siam and East Coast of Malaya.

Specimens examined: Unfederated Malay States: Kelantan: 4 ♂, Tebing Tinggi, vii.1920 (*V. Knight*). F.M.S. Museum's collection.

Federated Malay States: ♂, Pahang (no other data).

SIAM : ♂, Nakon Sri Tamarat (Nagorn Sridharmraj), Ronpibun, 18.ii.1932 (*H. M. Pendlebury*).

Mickel (1933, *Ann. ent. Soc. Amer.* **26** : 395) referred to *skeati* as the female of *malayana*, but in view of the lack of any direct evidence for associating the two subspecies he separated it again (1935, *Trans. R. ent. Soc. Lond.* **83** : 230). Since the female of *skeati* and the male of *malayana* are only known from the East Coast of the Malay Peninsula, and no other subspecies is known from that area, the association is probably correct. The only other subspecies known from Peninsular Malaya is *singapora* from Singapore Island and the West Coastal plain, and two undescribed females mentioned herein, both from Singapore Island, are included in my key as ? *singapora* Mickel. Subspecies *sunda* Mickel does not occur in Malaya proper, being confined to Java and, possibly, the nearby islands.

Timulla (*Trogaspidia*) *philippinensis sunda* Mickel.

Timulla (*Trogaspidia*) *philippinensis sunda* Mickel, 1935, *Trans. R. ent. Soc. Lond.* **83** : 229, ♂.

Holotype.—♂, JAVA : Soekaboemi, in Cornell University collection, Ithaca, New York.

The female of this subspecies is hitherto undescribed. Direct evidence is now available for associating the sexes, a number having been taken *in copula* by Dr. M. A. Lieftinck, who very kindly sent them to me for examination.

♀. Head, abdomen and legs, black ; thorax ferruginous ; second abdominal tergite with a pair of subcircular, pale pubescent spots, separated by a distance about equal to, or slightly less than, their greatest diameter ; third tergite with an interrupted fascia of pale, appressed pubescence ; fourth tergite with a pair of subquadrate spots of pale, appressed pubescence, separated by a distance slightly less than their transverse diameter ; pygidial area rugose, the rugosities tending to transverse, the apical sixth more finely so. Length 10·5 mm.

Head black, sculpture and pubescence as in subspecies *philippinensis* ; antennal tubercles and extreme apex of scape dark ferruginous ; pedicel and a varying number of flagellar segments more or less ferruginous beneath ; mandibles dark ferruginous medially, black at base and apex ; clypeus with the angles less strongly developed and the median tubercle smaller than in subspecies *philippinensis*.

Thorax clear ferruginous throughout, the sculpture and pubescence as in subspecies *philippinensis*. Scutellar scale moderately well developed.

Abdomen black, the second tergite with a pair of anterior, sub-circular spots of appressed, pale, glittering pubescence, separated from one another by a distance about equal to, or slightly less than, their greatest diameter ; third tergite clothed with dense, appressed, pale, glittering pubescence, the pale pubescence reaching the lateral margin, interrupted medially with black, the interruption widened anteriorly ; fourth tergite with a pair of large, transverse, subquadrate spots of appressed, pale pubescence, each spot about two-thirds as wide as its transverse diameter, separated by a distance slightly less than their transverse diameter, the spots not reaching the lateral margin ; first tergite with some sparse, erect, pale pubescence ; antero-lateral areas of second tergite with some sparse, erect, pale hairs, the hairs inconspicuous, the lateral margin with appressed, pale pubescence, felt line cupreous ; second and third sternites with an apical fringe of pale pubescence, that of sternites 4 and 5 black intermixed with some fuscous hairs ; all the sternites with some sparse, erect, pale pubescence ; pygidial area rugose throughout, the apical sixth more finely so, the rugosity tending to transverse.

Allotype.—♀, SOUTH JAVA: Banjoemas, Babakan, 27.iii.1933 (*M. A. Lieftinck*) taken *in copula* with ♂ and pinned on the same pin. In Zoölogisch Museum, Buitenzorg, Java.

Other specimens examined: SOUTH JAVA: ♀, Babakan, Z.K. 27.xi.1932 (*F. C. Drescher*); 5 ♂♀ *in copula* and 2 ♀, Banjoemas, Babakan, 27.iii.1933 (*M. A. Lieftinck*); ♂ Penandjoeng Bay, Tjimanak, vii.1936 (*M. A. Lieftinck*); ♀, Djeroeklegi zind Banjoemas, x.1936 (*F. C. Drescher*).

WEST JAVA: ♀, Palaboean ratoe, Tjisolok, 2.v.1932 (*M. A. Lieftinck*); ♂, Palaboean ratoe, Tjipanas, 16–17.iv.1933 (*M. A. Lieftinck*); ♂, Buitenzorg, 25.ii.1935 (*van der Goot*); ♂, Wynkoopsbaai, iii.1935 (*M. E. Walsh*); ♂, Djampang Tengah, Goenoeng Tjisoeroe, iii.1935 (*M. E. Walsh*); ♂, Djampang Tengah, viii.1935; 2 ♂, Palaboean ratoe, Tjisolok, xii.1935 (*F. Dupont*); ♂, Buitenzorg, Tjiboeria, 26.iv.1936 (*J. van der Vecht*); ♂, Depok, 17.i.1937 (*E. van der Vecht*); ♀, Preanger, Radjamandala (*G. Pantjalikan*), 400 m., v.1937 (*F. C. Drescher*); 4 ♂, Mts. Djampang Wetan, 1200 ft., Radjamandala, viii.1937 (*M. E. Walsh*); 2 ♂, Djampang, viii.1937 (*M. E. Walsh*); 3 ♂, Mts. Djampang Wetan, 1200 ft., Radjamandala, xi.1937 (*M. E. Walsh*); ♂, Buitenzorg, Tjibrangbang, Mt. Salak, 1200 ft., xi.1937 (*M. E. Walsh*); 2 ♂, Wynkoops, xi.1937 (*M. E. Walsh*).

EAST JAVA: ♂, Wadjak, i.1935 (*W. F. Jepson*); ♂, Wadjak, 20.i.1936 (*W. F. Jepson*).

MIDDLE JAVA: ♂, Karimon Djawa, v.1926 (*Dammerman*); ♂, Nglirip, Teak Forest near Bodjonegoro, i.1936 (*M. E. Walsh*).

JAVA (? district): ♂, Tjiboedeg bij Boland, 3.iii.1929; ♂, Baoeng, 350 m., viii.1935; ♂, Djembu, i.1936.

The females vary in size from 9 to 14 mm., with an average of 11·6 mm. The colour of the antennae is variable, some having the ferruginous parts of the allotype partly or wholly black. The relative size of the spots on the second tergite and the distance between them varies slightly, but the distance separating the spots is not greater than their greatest diameter. The occurrence of one doubtful female of this subspecies from Ardjasa in the Kangean Islands, which seem, otherwise, to have their own distinct subspecies, is remarkable. The female in question is too badly crushed for certain determination and has not been included in the list of specimens examined.

Timulla (Trogaspidia) philippinensis kangeana subsp. n.

♂. Very similar to subspecies *sunda* Mickel from which it is at once distinguishable by the very dark ferruginous colour of the abdomen and by the pubescence of tergites 2 to 6 also being very dark ferruginous or black. Sternites 1 and 2 bear some scattered, erect, pale hairs and sternites 2 to 5 have their apical fringes with a few pale hairs intermixed with the darker ones. This subspecies agrees with *sunda* in the impunctate, glabrous disc of the second tergite and in the rather weak clypeal ridge. The pubescence of the head, thorax and legs is similar to that of *sunda*. Length 22 mm.

♀. Differs from *sunda* in the much smaller pale pubescent spots, separated by at least their own diameter, on the second tergite, in the widely separated pale pubescent spots on the fourth tergite, in having the pale hairs of the first tergite and the antero-lateral areas of the second tergite in part appressed and thus more obvious than in *sunda*, and in the weaker scutellar scale. Length 13 mm.

Holotype.—♂, KANGEAN ISLANDS: Boejoetan, Teak Forest, 50–100 m., ii.1936 (*M. E. Walsh*). In collection of Dr. J. G. Betrem, Malang, Java.

Allotype.—♀, KANGEAN ISLANDS: Petapan (O. Kust), secondary jungle, ii.1936 (*M. E. Walsh*). In collection of Dr. J. G. Betrem, Malang, Java.

Paratypes.—KANGEAN ISLANDS: 4 ♂, Petapan (O. Kust), secondary jungle, ii.1936 (*M. E. Walsh*); ♂, Boejoetan, teak forest, ii.1936 (*M. E. Walsh*); ♂, Tembajangan, teak forest, ii.1936 (*M. E. Walsh*); 4 ♂, Paliat eiland, iii.1936 (no collector's name); 2 ♂, Aegsn-Kokap, Nord-kust, iii.1936 (*M. E. Walsh*).

Other specimens examined: a single ♀ without any data is attributable to this subspecies.

The ♂ paratypes vary from 17–24 mm. in length.

This subspecies appears to be quite distinct and can be readily picked out from among specimens of subspecies *sunda* without the use of any optical aids. Subspecies *sunda* may, however, extend to the Kangean Islands as is indicated by a much-crushed female, which appears to be *sunda*, labelled Ardjasa among material submitted by Dr. J. van der Vecht. Dr. van der Vecht informs me that this specimen was one of a consignment of papered insects from both the Kangean Islands and the mainland, sent to him at the same time, but he does not think it likely that it became mixed up with the wrong material. There is this slight element of doubt, however, which further collecting in these Islands will clear up.

The sexes have not been taken *in copula*, but it is extremely unlikely that there should be another subspecies in such a comparatively small area as the Kangean Islands and it seems safe to assume that the specimens recorded above are the sexes of one and the same subspecies.

Timulla (Trogaspidia) philippinensis paloeana subsp. n.

♂. Head, thorax and legs entirely, abdominal segments 1 and 5 mostly, 6 and 7 entirely, black; clothed with moderate, erect, and shorter, decumbent, sparse, black pubescence; disc of second tergite glabrous, impunctate; face with a considerable amount of pale pubescence; pronotum and dorsum of propodeon with black pubescence. Length 15 to 18 mm.

Head black, the lateral pubescence between the eyes and clypeus dense, decumbent and silvery; the tuft of hair above the clypeus tawny; the appressed pubescence between the antennal scrobes pale golden; the erect pubescence on the frons, particularly in the emargination of the eyes, very dark cupreous; erect pubescence on the vertex black, with a cupreous sheen basally, the pubescence becoming pale towards the occiput; pubescence on genae and head beneath pale tawny; mandibles clothed basally with short, decumbent, pale pubescence, interspersed with longer, erect, pale hairs; median longitudinal ridge of clypeus moderately elevated, much more so than in subsp. *philippinensis* and almost as much as in subsp. *singapora*.

Thorax black, with black pubescence; dorsum of pronotum clothed with sparse, erect and sub-erect, black pubescence, beneath which is a dense pile of very short, dark cupreous, pubescence posteriorly; sides of pronotum anteriorly with pale pubescence; mesonotum scutellum and metanotum with black pubescence, the lateral fovea of the scutellum and metanotum with fine, pale tawny pubescence; dorsum of propodeon with fine, sparse, decumbent, black pubescence, interspersed with sub-erect, black hairs; sides and posterior face of propodeon with sparse, long, erect, pale pubescence; prepectus with sparse, pale pubescence; mesopleura with sparse, erect, black pubescence on the dorsal third, the remainder with sparse, erect and sub-erect, pale tawny pubescence; metapleura micro-pubescent.

Abdomen clothed with sparse, black pubescence, except the base of the first tergite and the first sternite with pale pubescence, and the posterior margins of sternites 2 and 3 with a thin fringe of aeneous pubescence intermixed with black pubescence; first tergite black, indistinctly rufescent on the apical fourth; tergites 2 and 3 wholly ferruginous, disc of two impunctate; tergite 4 mainly ferruginous, but with a triangular, median, black suffusion, its apex anterior; tergite 5 black, except the anterior lateral thirds ferruginous; tergites 6 and 7 black; first sternite black, its carina high; second to fifth sternites ferruginous; remaining sternites black.

Legs black, clothed with pale pubescence, intermixed with cupreous pubescence on the tarsi beneath and on the intermediate and posterior tibiae above; calcaria pale.

Wings as in the other subspecies.

♀. Very similar to that of subspecies *sunda* Mickel described above, but differs in the strongly golden colour of the pale maculae and other pale pubescence. Sub-erect pubescence of the frons with rather strong coppery reflections; pale pubescence of genae and clypeus distinctly golden; median tubercle of clypeus feeble; apex of scape dark ferruginous; vertex with a subquadrate patch of dense, appressed, black pubescence on either side of the median line and extending to above the eye (present in other subspecies but not so marked).

Thorax clear ferruginous; scutellar scale only feebly indicated, slightly notched (but this may be inconstant).

Abdomen black, the pale pubescent spots of the second tergite large, subcircular, strongly golden, separated by a distance slightly less than their greatest diameter; felt line cupreous; pubescence of lateral margin of second tergite dense, pale golden; antero-lateral areas of second tergite with sparse, but conspicuous, erect and appressed pale hairs; third tergite clothed with dense, appressed, pale golden pubescence, slightly paler than the pubescence of the spots on the second tergite, widely interrupted medially with black; fourth tergite with a pair of large, subquadrate maculae of dense, appressed, pale golden pubescence, separated by a space slightly less than their transverse diameter, which is about equal to the lateral areas of black pubescence; fifth tergite with black pubescence; anal fringes pale golden; pygidial area rugose throughout, the apical sixth more finely so; apical fringe of second and third sternites dense, pale golden; that of the fourth and fifth black, interspersed with some pale hairs.

Legs black; calcaria pale ferruginous; tibiae with moderately dense, pale golden, recumbent pubescence, much more pubescent than in subspecies *sunda*. Length 12·5 mm.

Holotype.—♂. West Celebes: Paloe, xii.1936 (*native collector*). In Zoölogisch Museum, Buitenzorg, Java.

Allotype.—♀. West Celebes: Paloe, xii.1936 (*native collector*). In Zoölogisch Museum, Buitenzorg, Java.

Paratypes: 4 ♂, West Celebes: Paloe, xii.1936 (*native collector*).

The allotype is the only specimen of the female and it was not taken *in copula* with a male, but from a study of the females of subspecies *sunda*, which it closely resembles, and from the fact that it was taken in the same locality and at the same time as the males which I have associated with it, I do not think that there can be much doubt that it is correctly assigned here.

Timulla (Trogaspidia) philippinensis sumbana subsp. n.

♀. This subspecies more closely resembles subspecies *philippinensis* in that it has an entire, pale fascia on the third tergite. It differs from the other described females as follows: Anterior spots of second tergite small, pale, brassy, separated by one and one-half times their greatest diameter ; third tergite with an entire fascia, slightly, but distinctly, golden ; fourth tergite with a pair of small, subquadrate spots of appressed, pale golden pubescence, separated by a distance greater than their transverse diameter ; lateral rugae of pygidial area tending to longitudinal striae.

Legs black, the tibiae moderately densely clothed with pale, recumbent pubescence. Length 16 mm.

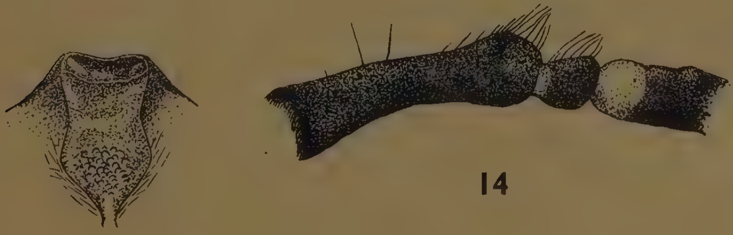
Holotype.—♀, Mao Marroe, 450 m. v.1935. (*K. W. Dammerman*). In collection Zoölogisch Museum, Buitenzorg, Java.

Timulla (*Trogaspidia*) *bataviana* (André).

Mutilla bataviana André, 1909, *Notes Leyden Mus.* **31** : 177, ♂.
Timulla (*Trogaspidia*) *bataviana* Mickel, 1935, *Trans. R. ent. Soc. Lond.* **83** : 250 : ♂.

Type.—♂, Java, in Leyden Museum.

Other specimens examined : East Java : Malang, 2 ♂, iii.1933 and iv.1933 (*Betrem*). West Java : 2 ♂, Gunong Tjampea, 250 m., 30.iv.1935 (*E. van der Vecht*).



Figs. 13–14.—(13)[2] Median area of clypeus of *T.* (*T.*) *bataviana* (André), ♂ ; (14) Scape, pedicel and first flagellar segment of right antenna of *T.* (*T*). *bataviana* (André), ♂.

Through the good offices of Mr. R. B. Benson of the British Museum (Natural History) I was able to examine the type while on leave in 1939 and to André's original description I would add the following, supplementary remarks :

Median area of clypeus in the form of an irregular, elongate pentagon, of which the lateral margins are slightly concave ; surface of median area feebly concave, highly polished and shining, except the dorsal third with minute, close, separate punctures and fine pubescence ; anterior margin feebly emarginate, with a broad, transverse, submarginal fovea.

Scape slightly twisted, dilated at base and apex, somewhat flattened beneath with two, widely separated carinae, which coalesce at the apex to form a single, prominent ridge ; space between the carinae polished, with a few, minute rugulosities ; apex of scape externally ferruginous, the inner angle with a small tuft of pale golden pubescence ; pedicel constricted basally, where it is luteous, flattened beneath and with a distinct fringe of pale

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[2] The pubescence has been omitted entirely in the drawings of the *erato* group and only the two rather obvious fringes of hairs are indicated in the drawing of the antenna of *bataviana*, though both scape and pedicel are pubescent.

golden pubescence on the inner margin ; first flagellar segment flattened, the basal third white ; rest of antennae black.

Dorsum of propodeon with appressed, pale golden glittering pubescence.

Second sternite with five distinct areas, the lateral ones triangular, densely, confluently punctate, separated from the three ventral ones by a distinct carina ; ventrally there are two latero-basal, flattened, confluently punctate areas, separated medially by a longitudinal, cariniform gibbosity, and a lunate posterior area, separated from the basal areas by a smooth, polished bevel, the area itself flattened and finely, longitudinally divergently rugulose, almost striate, along the posterior margin ; third to sixth sternites, with a few, fine, longitudinal rugulosities along the posterior margin medially ; third and fourth sternites simple ; fifth sternite black, with a pair of small, lateral, glabrous tubercles, defining a small, lateral, confluently punctate, triangular area ; sixth with a pair of strong, lateral, convergent carinae, extending from the extreme baso-lateral angle almost to the posterior margin, and demarcating a distinct, lateral, punctate area ; seventh with a similar structure, the ridges closer, the area between them concave, polished and shining ; hypopygium with a strongly elevated, glabrous and polished, lunate basal area, narrowed at the apex, where there is a small, median, subapical fovea, extending from the base to two-fifths, the structure apparently formed by the coalescing of a pair of ridges similar to those on the preceding sternite. Third to fifth tergites each with a distinct, wedge-shaped, lateral spot of appressed, golden pubescence.

Intermediate coxae distinctly flattened beneath, glabrous, polished and shining, except the posterior margin with sparse, pale pubescence ; posterior coxae slightly flattened beneath, wholly pubescent.

Length 6 mm. to 11 mm.

The remarkable form of the antennae, the five areas of the second sternite and the lateral armature of the fifth to seventh sternites are characters which appear to be unique.

Smicromyrme Thomson.

Smicromyrme kellyi Pagden.

Smicromyrme kellyi Pagden, 1934, *J. F.M.S. Mus.* **1** : 439, ♂♀.
Timulla (*Trogaspidia*) *kellyi* Mickel, 1935, *Trans. R. ent. Soc. Lond.* **83** : 267, ♂.
Smicromyrme kedahensis Mickel, 1935, *Trans. R. ent. Soc. Lond.* **83** : 290, ♀.

The above synonymy must now be published as the result of the capture of a male and female *in copula* on 18.viii.1940, by Mr. N. C. E. Miller of the Department of Agriculture, S.S. & F.M.S.

The pair were captured on a blade of *Imperata cylindrica* Beauv. (lallang grass) near the reservoir at Kuala Sleh, and were given to me while still alive.

While I have always had a strong feeling that my original association of the sexes of this species was correct it was impossible to be certain until direct biological evidence was obtained. The existing diagnosis of the genera *Smicromyrme* and *Trogaspidia* entirely justifies Professor Mickel's action in removing the male from *Smicromyrme* and placing it in *Trogaspidia*. Before writing this note I communicated with Professor Mickel on the subject and he has very kindly examined a number of other "*Trogaspidia*" males which have similar characteristics to the male of *kellyi* and has also sought for other characters which might be used in separating the two genera. In his reply to me he points out that the scape in *Smicromyrme* is relatively much shorter than in *Trogaspidia*, and that the pedicel is very short and disc-like, without distinct erect hairs, very similar in texture to the first flagellar segment, while in *Trogaspidia* the pedicel is not disc-like, though short, and is covered with erect, stiff hairs.

I am very grateful to Professor Mickel for pointing out these characters, which will certainly make it possible to place some rather doubtful males more correctly.

Some further locality records for this species can now be given: Malacca: Sungai Udang, ♀, 6.iii.36 (*H. T. P.*). Selangor: Serdang, 3 ♀, 3.iii.36, 26.viii.37, 13.xii.37 (*H. T. P.*); Bangi, 11.i.40 (*N. C. E. Miller*); Dengkil, 25.v.1940; Ampang Reservoir, 4 ♀, 9.vi.40 (*H. T. P.*). Pahang: Kuala Tahan, 12.iv.40 (*M. W. F. Tweedie*).

Smicromyrme athalia sp. n.

♂. Black, except the mandibles with a pre-apical ferruginous cloud, their apices piceous, and the tegulae testaceous, clothed with sparse, silvery pubescence, with a few, dark, erect hairs round the eyes. Wings clear at the base, slightly smoky towards the apex. Mandibles with a single pre-apical tooth, strongly excised beneath near the base. Clypeus depressed, but not below the surface of the mandibles, the margin produced in the median half, which is widely and very shallowly emarginate, clothed with moderately dense and moderately long, decumbent, silvery pubescence. Length 7·2 mm.

Head black, except the mandibles ferruginous on their inner surface and with a pre-apical ferruginous cloud externally, their apices piceous, clothed with sparse, long, erect, silvery pubescence interspersed with shorter, sub-erect pubescence on frons and vertex, long and decumbent pubescence on the clypeus, short and appressed pubescence round the posterior margin of the eyes, and with a few, long, erect, dark hairs round the eyes and on the occiput; frons and vertex longitudinally striate, with small, shallow punctures between the striae; emargination of the eyes with small, shallow, confluent punctures; genae and vertex with small, close, separate punctures; surface of genae between the punctures dull and microrugulose; clypeus depressed, the median portion of the margin very shallowly and widely emarginate, with a submarginal impression; surface of clypeus very finely and closely punctate; median area triangular, concave within, the lateral arms terminating just before the lateral angles of the production; scape distinctly bicarinate beneath, confluently punctate on the inner and dorsal surfaces and with exceedingly minute, separate punctures externally, clothed with sparse, silvery pubescence; pedicel and first flagellar segment black, clothed with short, downy pubescence; rest of flagellum microrugulose, the sculpture giving it a cinereous appearance; second flagellar segment about twice as long as the first, which is very short and only a little longer than the pedicel, third a little shorter than the second; antennal scrobes carinate above; ocelli in an isosceles triangle widest at the base, median ocellus about one and one-half times the diameter of a lateral ocellus; mandibles deeply excised beneath, forming a strong, blunt, conical tooth, their apices simple, with a single pre-apical tooth inwardly. Relative widths of head and thorax including the tegulae, 1·0 : 1·16 (micrometer reading 4·4 : 5·1).

Thorax black, except the tegulae testaceous, clothed with sparse, silvery pubescence, with a few darker hairs on the mesonotum; pronotum with moderately deep, small, close punctures, the surface polished except along the anterior margin, where it is dull and finely rugulose, sides of pronotum microreticulate, with a few longitudinal costae posteriorly, clothed on the dorsum with sparse, erect and shorter, decumbent, pale pubescence, the pubescence on the posterior margin more dense, laterally almost glabrous; mesonotum with moderate, close punctures, some of them confluent, the surface polished and shining, clothed with very sparse, sub-erect, pale pubescence anteriorly; medially, laterally and posteriorly with sub-erect, black pubescence; longitudinal impressions reaching nearly to the anterior margin; scutellum closely, confluently punctate, its lateral concavities with dense, appressed, pale pubescence ; metanotum rugulose, the lateral foveae filled with appressed, pale pubescence ; propodeon fairly evenly reticulate, with three basal areas filled with appressed, pale pubescence, without a well-defined median area, but with an irregular, median space on the basal third, clothed with very sparse, erect, and sparse, shorter, decumbent, pale pubescence ; prepectus finely rugulose ; mesopleura finely punctate and very finely rugulose, clothed with appressed, pale pubescence, interspersed with some longer, erect, pale hairs ; metapleura finely pubescent, polished and remotely micropunctate, the epimeron microrugulose ; sides of propodeon polished and shining, with broken reticulations towards the dorsum ; tegulae testaceous, polished and with a few scattered punctures anteriorly, clothed with pale pubescence anteriorly and along the inner margin.

Abdomen black, clothed with sparse, erect, pale, pubescence, except on the apical two-thirds of the sixth tergite and the whole of the seventh tergite, where the pubescence is black ; first and second tergites with a distinct, third to fifth with a less distinct, apical fringe of pale pubescence ; first tergite with a clear, polished space on the anterior slope, laterally and dorsally with moderate punctures, becoming finer towards the apical margin ; second tergite with moderate, separate punctures, coarse and close laterally, fine and close anteriorly and posteriorly, with a well developed felt line fuscous ; third to sixth tergites with very fine, close, separate punctures on the dorsum anteriorly, the rest with remote, moderately fine punctures, coarser and closer laterally ; tergites 3–5, and 6 anteriorly, clothed with sparse, erect, pale pubescence, decumbent and forming a thin fringe posteriorly and with short, sparse, decumbent pubescence on the anterior, finely punctate portion ; posterior half of sixth tergite with sparse, erect, black pubescence ; seventh tergite relatively coarsely, confluently punctate, with an ill-defined, elongate space medially, sides of space parallel, apical margin membranous, the tergite armed on the postero-lateral third with a short, glabrous ridge terminating at the lateral angle, clothed with sparse, erect and short, sub-erect, black pubescence ; first sternite confluently punctate, the carina long, low and spinosely produced posteriorly, clothed with sparse, erect, pale pubescence and with a thin, apical fringe of short, pale pubescence ; second sternite evenly curved, almost flat in profile, the extreme anterior face steeply sloped and with a median, finely punctate and slightly gibbous area on the brow, with moderate, separate punctures, more remote than on the tergite, with a short felt line about half way along the side, clothed with sparse, erect and sparse, decumbent, pale pubescence, and with a thin, apical fringe of pale pubescence ; third to sixth sternites transversely microstriate anteriorly, finely and closely punctate on the normally exposed surface, clothed with sparse, erect, pale pubescence, each with a very thin apical fringe, interrupted medially ; sixth sternite widely and shallowly emarginate ; seventh sternite moderately finely, closely punctate, clothed with sparse, erect and more dense, decumbent, fuscous pubescence.

Wings sub-hyaline, infuscate apically, veins piceous ; cell R_5 receiving vein M_{3+4} slightly before the middle ; cell $R + 1st\ R_1$ longer than cell $2nd\ R_1 + R_2$.

Legs black, except the anterior coxae, trochanters, and the extreme base of the femora tinged ferruginous, clothed with pale pubescence ; calcaria pale ; tarsal pecten testaceous ; claws ferruginous.

♀. Head black, except clypeus, basal two-thirds of mandibles, antennal tubercles, scape and part of flagellum beneath, ferruginous, with a more or less rectangular patch of golden pubescence on the vertex ; thorax ferruginous, with a small wedge of pale, glittering pubescence at the promesonotal angles ; abdomen black, except the first segment more or less ferruginous, the second tergite with three spots of appressed, glittering pubescence, the median spot golden, the lateral ones silvery ; third tergite wholly clothed with appressed, pale, glittering pubescence ; fourth similar, but widely interrupted medially with black ; pygidial area strongly, longitudinally and divergently striate on the basal two-thirds ; legs variegated with ferruginous and piceous. Length 6 mm.

Head black, except the basal two-thirds of the mandibles, the clypeus, antennal tubercles, scape, pedicel and first two flagellar segments, dark ferruginous ; clothed with sparse, erect, dark hairs on the frons, vertex and genae, interspersed on the frons with shorter, sparse, sub-erect, piceous pubescence, except above the antennae, where this pubescence is golden; vertex with a more or less rectangular spot of sparse, decumbent, golden pubescence, about three-quarters as wide as the vertex; genae with sparse, appressed, pale, glittering pubescence; mandibles simple, their apices piceous; clypeus feebly emarginate medially, the median area in the form of a narrow, raised triangle, with a small, median tubercle; base of mandibles and clypeus with sparse, pale golden hairs; antennal tubercles ferruginous, glabrous, shining and with one or two shallow punctures; scape ferruginous, shining, with a few shallow punctures and clothed with sparse, decumbent, pale, glittering pubescence; pedicel and first flagellar segment ferruginous, second ferruginous beneath, piceous above, the rest shading through piceous to black; first and second flagellar segments subequal; antennal scrobes carinate above; frons moderately coarsely punctate, confluently just above the antennae, the punctures distinct and separate above, becoming finer towards the vertex; vertex finely, closely, confluently punctate; genae with fine, close, separate punctures; gula finely transversely striate; malar space with fine, separate punctures. Relative widths of head and thorax 1·2 : 1·0 (micrometer reading 4·2 : 3·5).

Thorax ferruginous, narrowed medially, humeral angles rounded and about as wide as posterior angles; coarsely, confluently punctate, with a wide, but low, polished scutellar scale, on either side of which are a few scale-like denticles; dorsum of propodeon confluently punctate on the basal two-thirds, posteriorly polished, with a few, shallow punctures at the base and minute, close, separate punctures apically; dorsum of thorax clothed with sparse, erect, bristle-like, dark hairs and closer, decumbent, dark pubescence, interspersed with some glittering, coppery pubescence; pro-mesonotal angles with a small wedge of appressed, pale, glittering pubescence; dorsum of propodeon with sparse, erect, pale pubescence; sides of pronotum micropunctate; prepectus longitudinally microrugulose, with a few shallow punctures posteriorly; meso- and metapleura microrugulose above, microreticulate below, clothed on the ventral third with appressed, pale, glittering pubescence; sides of propodeon shining, with a few, scattered, fine, shallow punctures above, micropunctate ventrally.

Abdomen black, except the first segment ferruginous, its tergite apically piceous; the whole of the first segment, and the rest of the abdomen beneath and laterally, clothed with very sparse, moderately long, erect, pale pubescence; second tergite with very sparse, erect, black pubescence; tergites 3–5 with mixed, erect pubescence; first tergite with moderate, confluent punctures laterally, separate dorsally, micropunctate between, with a thin apical fringe of long, pale hairs; second tergite with dense, moderate punctures, finer laterally, confluent basally and dorsally, densely clothed with decumbent, black pubescence and decorated with three oval spots of dense, appressed, glittering pubescence, arranged in a transverse line slightly anterior to the middle, the lateral spots silvery, the median one larger and golden; felt line fulvous; apex of tergite impressed, impunctate, without a fringe; third tergite entirely clothed with dense, appressed, pale, glittering golden pubescence, finely and densely punctate where the sculpture is visible, the margin impressed and impunctate; fourth tergite finely and densely punctate, clothed with appressed, pale, glittering pubescence on the lateral thirds, the median third with appressed, black pubescence, narrowed anteriorly, margin impressed, impunctate; fifth tergite finely and densely punctate, clothed with appressed, black pubescence, except extreme laterally the pubescence long and pale, margin impressed, impunctate; sixth tergite finely and densely punctate laterally at the base, with a lateral pencil of fulvous hairs; pygidial area defined by a carina, strongly, longitudinally and slightly divergently striate on the basal two-thirds, apical third polished and shining; first sternite finely rugulose, the carina feeble and only slightly elevated posteriorly; second sternite with moderate, separate punctures, finer laterally, with a feebly concave area antero-laterally, the anterior margin with a triangular area, finely and densely punctate and finely pubescent on the brow, clothed with a sparse, erect and sparse, sub-erect, pale pubescence and with a thin apical fringe of pale pubescence; third to fifth sternites finely, transversely striate extreme basally, minutely and remotely punctate medially, finely and densely punctate, apically clothed with sparse, erect, pale pubescence and with a thin apical fringe of pale pubescence; sixth sternite finely, transversely striate extreme basally, finely and densely punctate except the extreme apex impunctate, with erect, pale pubescence; second to fifth sternites with the margin impressed, impunctate.

Legs.—Coxae and trochanters ferruginous; anterior femora, tibiae, metatarsi and last tarsal segment piceous, tarsal segments 2–4 ferruginous; intermediate femora and tibiae piceous, except the base for at least one-third ferruginous; intermediate and posterior tarsi dark ferruginous; clothed with sparse, pale pubescence, that on the tarsi beneath somewhat fulvous; calcaria pale.

Holotype.—♂. Federated Malay States: Kuala Lumpur, 24.v.1936 (No. 0242) (*H. T. Pagden*). In Selangor Museum, Kuala Lumpur, F.M.S.

Allotype.—♀. Federated Malay States: Kuala Lumpur, 23.v.1936 (No. 0240) (*H. T. Pagden*). In Selangor Museum, Kuala Lumpur, F.M.S.

Paratypes. Federated Malay States: ♂, Kuala Lumpur, on bamboo, 24.ii.1928 (No. 142); 2 ♂, Kuala Lumpur, on bamboo, 4.iii.1928 (Nos. 269 and 270); ♂, Kuala Lumpur, on *Bambusa nana*, 12.iii.1928 (No. 319); ♂, Serdang, Selangor, on *Citrus limon*, 16.iii.1928 (No. 341); ♂, Kuala Lumpur, at light, 22.iii.1928 (No. 368); ♀, Serdang, Selangor, on lemon leaf, 18.iv.1948; ♂, Kuala Lumpur, on *Bambusa nana*, 19.ix.1928 (No. 880); ♂, Ulu Klang, Selangor, 25.viii.1929 (No. 1221); 3 ♂ and 1 ♀, Selayang, Selangor, 12.x.1929 (Nos. 1317, 1318, 1320 and 1321); ♀, Kuala Lumpur, 8.xi.1935 (No. 038); ♀, Kuala Lumpur, 17.xi.1935 (No. 051); 2 ♀, Kuala Lumpur, 18.00 hrs., 2.ii.1936 (Nos. 087, 088); 5 ♀, Kuala Lumpur, 18.30 hrs., 3.ii.1936 (Nos. 089–093); ♀, Kuala Lumpur, 08.30 hrs., 8.ii.1936 (No. 096); 3 ♀, Kuala Lumpur, 18.30 hrs., 9.ii.1936 (Nos. 099–0101); 3 ♀, Kuala Lumpur, 17.30 hrs., 15.ii.1936 (Nos. 0103–0105); 3 ♀, Kuala Lumpur, 15.30 hrs., 22.ii.1936 (Nos. 0123–0125); ♀, Kuala Lumpur, 18.iii.1936 (No. 0133); 4 ♀, Kuala Lumpur, 26.iv.1936 (Nos. 0210–0213); 3 ♀, Kuala Lumpur, 29.iv.1936 (Nos. 0214–0216); ♀, Kuala Lumpur, 6.v.1936 (No. 0234); ♂, Kuala Lumpur, 24.v.1936 (No. 0243). All collected by the author. In some cases the time of capture is given, as this species seems to be active later in the day than others.

It is perhaps dangerous to assume the sexes to be of the same species in the absence of any direct biological evidence. A careful search has, however, been made wherever the female has been abundant and, except in one instance, the only male *Smicromyrme* found were of the species described above.

Smicromyrme decora (Smith).

Mutilla decora Smith, 1879, *Descr. new Sp. Hym.*: 200, ♀.
Mutilla decora Dalle Torre, 1897, *Cat. Hym.* **8**: 30, ♀.
Mutilla decora André, 1903, *Gen. Insect.* **11**: 39, ♀.
Smicromyrme decora Pagden, 1934, *J. F.M.S. Mus.* **17** (3): 465, ♂♀.
Smicromyrme decora Mickel, 1935, *Trans. R. ent. Soc. Lond.* **83**: 288, ♀.

Holotype.—♀, Straits Settlements: Penang Island. In British Museum (Natural History).

So far no description of the male has appeared, though I recorded a host of this species and mentioned the fact that I had obtained a mating between the sexes in 1934, *J. F.M.S. Mus.* **17** (3) : 465. At that time I was uncertain whether this male might not have been described under another name. Since that time I have not been able to find any described species which agrees with the males herein dealt with. I have submitted my specimens to Professor Clarence E. Mickel, who has very kindly examined them and reported that he was unable to ascribe them to any known species. It seems desirable, therefore, to record the discovery of the male more exactly than I have hitherto done, and to place on record a description. A redescription of the female, based on the type specimen and on fresh material, may aid in the exact determination of this rather common species.

♀. *Head* black, finely, confluently punctate medially, the punctures separate, on the frons laterally and on the vertex, clothed with very sparse, erect, black pubescence on the frons, vertex and just behind the eyes, with sparse, erect pale pubescence on the post-vertex and occiput and with sparse, decumbent, aeneous pubescence between the black pubescence on the frons and vertex ; genae with close, separate punctures and sparse, decumbent, pale pubescence ; antennal scrobes feebly carinate above ; antennal tubercles, scape, pedicel and first flagellar segment light ferruginous, second flagellar segment dusky ferruginous, the remainder black (in the type the third flagellar segment is dusky ferruginous, the remaining segments dark fuscous, paler beneath) ; clypeus light ferruginous, the median area very narrowly triangular, strongly raised, terminating in a median, submarginal tubercle ; margin of clypeus transverse, evenly rounded laterally ; mandibles pale ferruginous, their apices piceous, simple, with a single, feeble, pre-apical tooth on their inner margin ; cheeks beneath with a moderate, obtuse, dentiform tubercle near the mandibular articulation.

Thorax ferruginous, with dense, moderately small, confluent punctures ; scutellar scale small, rather variable, flattish and narrowed posteriorly ; clothed with very sparse, erect, black pubescence and sparse, short, decumbent, pale aeneous pubescence ; thorax evenly narrowed posteriorly, the lateral margins of the dorsum somewhat crenulate ; propodeon steeply rounded from the dorsum, shallowly reticulate on the brow, feebly longitudinally rugulose and with a few, small, sparse punctures posteriorly, with sparse, erect, pale pubescence ; thorax laterally micropunctate and micropubescent, with a patch of decumbent, pale, glittering pubescence above the intermediate coxae.

Abdomen black, with dark bluish reflections on the second tergite ; first tergite ferruginous, with sparse, fine, shallow punctures and sparse, erect, pale pubescence ; second tergite as above, with dense, small, separate punctures, somewhat confluent medially, with a small, anterior, median spot of appressed, pale pubescence, clothed with sparse, erect and more dense, decumbent, black pubescence and with some very fine, decumbent, pale pubescence, the posterior margin with a moderately broad fascia, widened medially, of appressed, pale, glittering pubescence, finely and densely punctate beneath the pubescence ; third tergite with a broad fascia of appressed, pale, glittering pubescence, finely and densely punctate beneath the pubescence ; fourth and fifth tergites with very fine, close, even punctures, closer on the fourth, and sparse, erect and sub-erect, black pubescence ; last tergite with small, moderately close punctures laterally ; pygidial area elongate, fusiform, piceous and shining, not carinate laterally ; pygidial fringes fulvous ; first sternite pale ferruginous, the carina low, clothed with sparse, erect, pale pubescence ; second sternite with moderately large, well separated, even punctures, clothed with sparse, erect and sparse, decumbent, pale pubescence and with a thin apical fringe of pale pubescence ; third to sixth sternites with fine, close punctures, finely transversely strigulose basally, with sparse, erect, pale pubescence and with a thin, apical fringe of pale pubescence on three to five.

Legs ferruginous throughout, with sparse, pale pubescence ; calcaria pale.

Relative widths of head and thorax anteriorly 1·25 : 1·0 (6·0 : 4·8 divisions of micrometer).

Specimens vary in length from 3 to 5·2 mm.

♂. Head and thorax, except the tegulae, the legs and the last four abdominal segments, black; first three abdominal segments more or less ferruginous; tegulae testaceous; clothed throughout with sparse, pale pubescence; wings hyaline, faintly infuscate apically. Length 6 mm.

Note.—The allotype is chosen as the specimen which copulated with a female in captivity; it differs from the other males in having the last five abdominal segments black.

Head black, clothed with sparse, erect, pale pubescence on the vertex and posteriorly, with sparse, sub-erect, pale pubescence on the frons and genae; clypeus with rather more dense, decumbent, pale pubescence; frons medially with very fine, not very close, punctures between the striae, which are fine, the punctures larger and sparser laterally; vertex polished and shining, with sparse, small punctures; genae with moderately small, confluent punctures, dull; ocelli in an isosceles triangle, widest at the base, the lateral ocelli nearly five times as far from the eye as their greatest diameter, and nearly twice as far from each other as their diameter (5 : 24 and 13 : 24 respectively); antennal scrobes feebly, but distinctly, carinate above; scape bicarinate beneath; first flagellar segment one-half as long as the second; median area of clypeus triangular, slightly raised, sub-carinate above at the apex of the triangle, depressed at the base submarginally, the lateral area shallowly concave; margin medially transverse; the whole clypeus very finely punctate, clothed with decumbent, pale pubescence; mandibles slightly expanded, but not excised, near the base beneath; apex of mandibles simple, with two, small, pre-apical teeth on their inner margin, the teeth and a moderately broad pre-apical area, rufo-testaceous, the rest of the mandibles black. Relative widths of head and thorax, including the tegulae 1·0 : 1·12 (8·5 : 9·5 divisions of micrometer).

Thorax black, except the tegulae dark testaceous, clothed with sparse, erect and sub-erect, pale pubescence, and sparse, decumbent pubescence on the pronotum, mesopleura, lateral fovea of scutellum and metanotum, and the extreme base of the propodeon; pronotum with moderately large, shallow, confluent punctures; mesonotum with smaller, confluent punctures, the surface shining; propodeon reticulate, with a short, broad, median basal area, and two lateral basal areas filled with decumbent, pale pubescence; sides of pronotum micropunctate, shining and micropubescent, the anterior margin carinate; mesopleura micropunctate and micropubescent anteriorly, moderately coarsely, confluently punctate, with sparse, erect and moderately dense, decumbent, pale pubescence on the convexity, micropunctate along the posterior margin; metapleura with the epimeron somewhat dull, micropunctate and micropubescent, the episternum shining, very remotely micropunctate and micropubescent, shallowly reticulate in the ventral third; sides of propodeon shallowly reticulate, except the anterior margin micropunctate and micropubescent; tegulae dark testaceous, paler and translucent posteriorly, shining, finely and remotely punctate except on the disc, two-thirds as wide as long.

Abdomen black, except segments 1 and 2 in the allotype ferruginous (other specimens have segment 3 more or less ferruginous, if less then suffused with blackish postero-medially) clothed with sparse, erect, pale pubescence on tergites 1–5, and on all the sternites; first tergite ferruginous with fine, remote punctures and sparse, erect, pale pubescence; second tergite with moderately fine, close punctures at the base laterally, finer and remote punctures dorsally, fine and close punctures apically, the surface polished, with a feeble, transverse, sinuate ridge at the posterior fifth, clothed with sparse, sub-erect, pale pubescence and a few, erect, pale hairs laterally and apically; third tergite wholly black in the allotype, ferruginous or ferruginous with a black, median, apical suffusion in all other specimens examined, with fine, moderately close punctures laterally, very fine, sparse punctures medially, clothed with sparse, erect, pale pubescence; fourth to sixth tergites black, puncturation as on the third, but finer, clothed with sparse, erect, pale pubescence, except the sixth with black pubescence; last tergite with a wide, flattened, triangular, glabrous, polished area, finely, remotely and evenly punctured laterally and basally, clothed with sparse, erect, black pubescence ; first sternite ferruginous, with a few, small punctures and sparse, erect, pale pubescence, the carina long, scarcely elevated ; second sternite ferruginous, with moderately small, sparse, even punctures, sparse, erect and sub-erect, pale pubescence and a thin, apical fringe of pale pubescence ; third sternite black in the allotype, ferruginous in all other specimens examined ; third to sixth sternites with small, close punctures on the apical half, very small, sparse punctures basally, sparse, erect and sub-erect, pale pubescence and a thin apical fringe of pale pubescence ; hypopygium simple, flat, with moderately even, small punctures and sparse, erect and sub-erect, fuscous pubescence.

Legs black, except the anterior tibiae and tarsi dark fuscous and all the trochanters castaneous, clothed with sparse, pale pubescence ; calcaria pale.

Wings hyaline, slightly infuscate apically ; cell R_5 receiving vein M_2 slightly beyond the middle ; vein R_4 sub-interrupted near its junction with vein M_1 ; cells R_4 and 1st M_2 nearly obsolete ; cells R + 1st R_1 and 2nd R_1 + R_2 subequal in length.

Length : allotype 6 mm., other specimens from 6 to 8 mm.

Allotype.—♂, FEDERATED MALAY STATES : Selangor, Kuala Lumpur, 27.ii.1928 (No. 252) ; captured flying round a hedge of *Bambusa nana* and copulated in captivity with a ♀ bred from the nest of *Pison argentatum* Shuck. (*H. T. Pagden*). In Selangor Museum, Kuala Lumpur, F.M.S.

Specimens examined.—FEDERATED MALAY STATES, STATE OF SELANGOR : ♂, Kuala Lumpur, *ex* cocoon *Pison argentatum* Shuck., 28.i.1928 (No. 23) (*H. T. Pagden*) ; ♂, Kuala Lumpur, *ex* cocoon *Pison argentatum* Shuck. 29.i.1928 (No. 24) (*H. T. Pagden*) ; 2 ♂, Kuala Lumpur, *ex* cocoons *Pison argentatum* Shuck., 1.ii.1928 (Nos. 36 and 37) (*H. T. Pagden*) ; 2 ♂, Kuala Lumpur, *ex* cocoons *P. argentatum* Shuck., 3.ii.1928 (Nos. 40 and 41) (*H. T. Pagden*) ; ♂, Kuala Lumpur, *ex* cocoon *P. argentatum* Shuck., 6.ii.1928 (*H. T. Pagden*) ; ♀, Kuala Lumpur, *ex* cocoon *P. argentatum* Shuck., 26.ii.1928 (No. 248), copulated with a ♂ allotype (*H. T. Pagden*) ; ♂, Serdang, on lemon bush, 22.iii.1928 (No. 367) (*H. T. Pagden*) ; ♂, Serdang, 27.iv.1928 (*H. T. Pagden*) ; ♀, Serdang, 6.vii.1928 (No. 685) (*H. T. Pagden*) ; ♀, Puchong, 28.x.1928 (No. 931) (*H. T. Pagden*) ; ♂, Ulu Gombak, xii mile, 7.iv.1929 (No. 1029) (*H. T. Pagden*) ; ♀, Kuala Lumpur, 16.i.1930 (No. 1504) (*H. T. Pagden*) ; ♀, Kuala Lumpur, 9.xi.1935 (No. 040) (*Mohammed Salleh*) ; ♀, Kuala Lumpur, 4.xii.1936 (No. 0345) (*H. T. Pagden*) ; ♀, Kuala Lumpur, Botanic Gardens, 1.ii.1937 (No. 0347) (*Mohammed Salleh*) ; ♀, Kuala Lumpur, Spooner Road, 27.v.1937, in house (No. 0374) (*H. T. Pagden*) : ♀, Serdang, 26.viii.1937 (No. 0392) (*Adbul Talib*).

STATE OF PERAK : ♀, Parit Buntar, in garden, 5.iv.1931 (No. 2040) (*H. T. Pagden*) ; ♀, Parit Buntar, 2.ix.1931 (No. 2313) (*H. T. Pagden*) ; ♀, Selama S.O.S. Estate, 19.ix.1931 (No. 2410) (*H. T. Pagden*) ; ♀, Parit Buntar, under house, 26.ix.1931 (No. 2427) (*H. T. Pagden*) ; ♀, Parit Buntar, under house, 18.xi.1931 (No. 2490) (*H. T. Pagden*).

NEW RECORDS OF MUTILLIDAE.

Squamulotilla Bischoff.

Squamulotilla deserta (Smith).

Mutilla deserta Smith, 1879, *Descr. new. Sp. Hym.* : 200, ♀.
Mutilla deserta Dalle Torre, 1897, *Cat. Hym.* 8 : 30, ♀.

Mutilla deserta André, 1903, *Gen. Insect.* **11** : 39, ♀.
Squamulotilla deserta Mickel, 1934, *Philipp. J. Sci.* **54** (1) : 109, ♀.
Squamulotilla deserta Mickel, 1935, *Trans. R. ent. Soc. Lond.* **83** : 193, ♀.

Holotype.—♀, CELEBES : in British Museum (Natural History).

Specimens examined.—JAVA : ♀, Malang, 21.ii.1933 (*Betrem*) ; ♀, Malang, March 1933 (*Betrem*) ; ♀, Malang, April, 1933 (*Betrem*).

KANGEAN ISLANDS : ♀, Nglirip, Teak Forest, i.1936 (*M. E. Walsh*).

I have not compared these specimens with the type, but they appear to agree entirely with it.

Distribution.—CELEBES, PHILIPPINE ISLANDS, JAVA, KANGEAN ISLANDS.

Squamulotilla aesyca (Cameron).

Mutilla aesyca Cameron, 1902, *Entomologist* **35** : 208, ♀.
Squamulotilla aesyca Mickel, 1935, *Trans. R. ent. Soc. Lond.* **83** : 194, ♀.

Holotype.—♀, BORNEO : in British Museum (Natural History).

Specimen examined.—WEST JAVA : ♀, Mt. Gedeh, Tapos, 1–6.viii.1936 (*J. van der Vecht*). In coll. J. van der Vecht.

I have examined the type specimen and a specimen determined by Mickel as this species and I am unable to find any reason for separating the specimen before me from either of the specimens examined. There are some slight differences in colour, but not sufficient even to warrant making this into a subspecies.

Odontomutilla Ashmead.

Odontomutilla familiaris familiaris (Smith).

Mutilla familiaris Smith, 1858, *J. Proc. linn. Soc.* (*Zool.*) **2** : 84, ♀.
Mutilla familiaris Dalle Torre, 1897, *Cat. Hym.* **8** : 39, ♀.
Mutilla familiaris André, 1903, *Gen. Insect.* **11** : 70, ♀.
Odontomutilla familiaris Mickel, 1934, *Philipp. J. Sci.* **54** (1) : 132, ♀, ♂.
Odontomutilla familiaris familiaris Mickel, 1935, *Trans. R. ent. Soc. Lond.* **83** : 201, ♀, ♂.

Holotype.—♀, MALAY PENINSULA : Singapore, in Saunders' coll., Hope Department, University of Oxford.

Allotype.—♂, PHILIPPINE ISLANDS : Dapitan, Mindanao (Baker), in United States National Museum.

Specimens examined.—MALAY PENINSULA : ♀, Trusan, 1889, in coll. F.M.S. Museums, Kuala Lumpur.

EAST BORNEO : ♂, Pelawan, v.1937 (*M. E. Walsh*) ; ♂, Batan Bessi, 150 ft., v.1937 (*M. E. Walsh*) ; ♂, Batan Bessi, vi.1937 (*M. E. Walsh*).

SOUTH BORNEO : ♂, near Tanggarong, 100 ft., 4.vii.1937 (*M. E. Walsh*).

Distribution.—MALAY PENINSULA, BORNEO, PHILIPPINE ISLANDS.

Odontomutilla haematocephala (André).

Mutilla simplicifascia var. *haematocephala* André, 1896, *Termes. Fuzetek* **19** : 16, ♂.
Odontomutilla simplicifascia var. *haematocephala* André, 1903, *Gen. Insect.* **11** : 29, ♂.
Odontomutilla haematocephala Mickel, 1935, *Trans. R. ent. Soc. Lond.* **83** : 213, ♂.

Holotype.—♂, Federated Malay States, Perak (*vide* Mickel, 1935).

Specimens examined.—FEDERATED MALAY STATES : ♂, Pahang, Fraser's Hill, 9.iii.1929 (*N. C. E. Miller*) (No. 1022), det. C. E. Mickel. In collection H. T. Pagden.

Straits Settlements : ♂, Penang, 1500–2428 ft., v.1917. In collection F.M.S. Museums.

S. Sumatra.—♂, Res. Bencoelen, Bukit Item, 650 m., 1935 (*M. E. Walsh.*) In collection J. van der Vecht.

Distribution.—Malay Peninsula, Sumatra.

Odontomutilla herpa (Cameron).

Mutilla herpa Cameron, 1902, *J. Straits Br. R. asiat. Soc.* **37** : 73, ♂.
Odontomutilla herpa Mickel, 1935, *Trans. R. ent. Soc. Lond.* **83** : 208, ♂.

Holotype.—♂, Borneo : Sarawak, in British Museum (Natural History).

Specimens examined.—Sarawak : ♂, Baram River, Gunong Tanabo, 10.xi.1920 (*J. C. Moulton*). In collection F.M.S. Museums.

Distribution.—Sarawak.

Odontomutilla manifesta (Smith).

Mutilla manifesta Smith, 1859, *J. Proc. linn. Soc.* (*Zool.*) **3** : 150, ♀♂.
Mutilla manifesta André, 1896, *Ann. Mus. civ. Stor. nat. Genova* **17** (2) : 69, ♀.
Mutilla manifesta Dalle Torre, 1897, *Cat. Hym.* **8** : 57, ♀♂.
Mutilla manifesta André, 1898, *Ann. Soc. ent. Fr.* **67** : 71, ♂.
Mutilla manifesta Mantero, 1900, *Ann. Mus. civ. Stor. nat. Genova* **40** : 583.
Odontomutilla manifesta André, 1903, *Gen. Insect.* **11** : 29, ♀♂.
Odontomutilla manifesta Mickel, 1935, *Trans. R. ent. Soc. Lond.* **83** : 207, ♀♂.

Holotype.—♀, and allotype ♂, Aru Islands. In Saunders' collection, Hope Department, University of Oxford.

Specimens examined.—♂, New Guinea : Pionierbivak, xii.1920 (*W. C. van Heurn*). In collection Buitenzorg Museum, Java.

Distribution.—Aru Islands, New Guinea.

Odontomutilla rubrocapitata Mickel.

Odontomutilla rubrocapitata Mickel, 1935, *Trans. R. ent. Soc. Lond.* **83** : 208, ♂.

Holotype.—♂, Borneo : Sandakan (Baker). In United States National Museum.

Specimens examined.—Federated Malay States : 2 ♂, Perak, Gunong Kledang, 2646 ft., xi.1916 ; ♂, Perak, Batang Padang, Jor Camp, 1800 ft., 4.vi.1923 (*H. M. Pendlebury*) ; ♂, Selangor, Bukit Kutu, 2500 ft., 20.iv.1926 (*H. M. Pendlebury*). All in collection Federated Malay States Museums.

Distribution.—Borneo, Federated Malay States.

Odontomutilla thymele Mickel.

Odontomutilla thymele Mickel, 1935, *Trans. R. ent. Soc. Lond.* **83** : 211, ♀.

Holotype.—♀, Borneo : Bettotan near Sandakan, vii.30.1937 (*C. Boden Kloss* and *H. M. Pendlebury*). F.M.S. Museum, Kuala Lumpur.

Specimens examined.—Borneo : ♀, Sarawak, Kuching, 17.v.1900. Both in collection F.M.S. Museums, Kuala Lumpur.

Distribution.—Borneo.

Odontomutilla urania (Smith).

Mutilla urania Smith, 1858, *J. Proc. linn. Soc.* (*Zool.*) **2** : 83, ♀ (*nec* ♂).
Mutilla urania André, 1896, *Termes. Fuzetek* **19** : 12, ♀.
Mutilla urania Dalle Torre, 1897, *Cat. Hym.* **8** : 94, ♀ (*nec.* ♂).
Mutilla urania André, 1898, *Ann. Soc. ent. Fr.* **67** : 31, ♀ (in part).
Odontomutilla urania André, 1903, *Gen. Insect.* **11** : 30, ♀ (in part).
Odontomutilla urania Mickel, 1935, *Trans. R. ent. Soc. Lond.* **83** : 213, ♀.

Holotype.—♀, MALAY PENINSULA : Mt. Ophir. In Saunders' collection, Hope Department, University of Oxford.

Specimens examined.—MALAY PENINSULA : ♀, *ex* coll. Dept. Agriculture (no other data) ; ♀, Perak, Gunong Kledang, 2646 ft., xi.1916 ; ♀, Kedah, Jitra, Catchment area, 10.iv.1928 (*H. M. Pendlebury*). All in collection F.M.S. Museums.

Odontomutilla cassiope (Smith).

Mutilla cassiope Smith, 1858, *J. Proc. linn. Soc.* (*Zool.*) **2** : 86, ♀.
Mutilla cassiope Dalle Torre, 1897, *Cat. Hym.* **8** : 21, ♀.
Odontomutilla cassiope André, 1903, *Gen. Insect.* **11** : 29, ♀.
Odontomutilla cassiope Mickel, 1935, *Trans. R. ent. Soc. Lond.* **83** : 216, ♂♀.

Holotype.—♀, BORNEO : Sarawak. In Saunders' collection, Hope Department, University of Oxford.

Allotype.—♂, BORNEO : British North Borneo, Bettotan, near Sandakan, 23.viii.1927 (*C. Boden Kloss* and *H. M. Pendlebury*). In collection F.M.S. Museums, Kuala Lumpur.

Specimens examined.—FEDERATED MALAY STATES : ♀, No. 600, Selangor, Ulu Gombak, 12th mile from Kuala Lumpur, 20.vi.1928 (*H. T. Pagden*) ; ♀, No. 701, Selangor, Ulu Gombak, 12th mile from Kuala Lumpur, 8.vii.1928 (*H. T. Pagden*) ; 5 ♂, Nos. 0620–0624, Selangor, Ampang pipe line, on leaves of shrub, 9.vi.1940 (*H. T. Pagden*) ; 3 ♂ and 1 ♀, Nos. 0659–0662, Selangor, Ampang pipe line, on leaves of shrub, 13.vi.1940 (*H. T. Pagden*).

DUTCH SOUTH BORNEO.—♂, Gunong Panjang, near Tenggarong, ± 150 ft , Mahakam River, 2.vii.1937 (*M. E. Walsh*).

All in collection H. T. Pagden.

Timulla (*Trogaspidia*) *celebensis* (André).

Mutilla celebensis André, 1905, *Z. Hymen. Dipt.* **5** : 215, 265. ♂♀.
Timulla (*Trogaspidia*) *celebensis* Mickel, 1935, *Trans. R. ent. Soc. Lond.* **83** : 266, ♂♀.

Holotype and allotype.—♂♀, SOUTH CELEBES : Bui-Kraeng, in Hungarian National Museum, Budapest.

Specimen examined.—♂, S.W. CELEBES : Gunong Lompo Batang, 1600 m., 1936 (*L. J. Toxopeus*). In collection Zoölogisch Museum, Buitenzorg. Java.

Timulla (*Trogaspidia*) *amans amans* (André).

Mutilla amans André, 1909, *Notes Leyden Mus.* **31** : 173, ♀ and ♂.
Timulla (*Trogaspidia*) *amans* Mickel, 1935, *Trans. R. ent. Soc. Lond.* **83** : 236, ♀♂.

Lectotype.—♀, JAVA : Tandjong Priok, iv.1908 (*M. E. Jacobson*), in Leyden Museum (before the war).

Allotype.—♂, JAVA : Tandjong Priok, iv.1908 (*M. E. Jacobson*), in Leyden Museum (before war).

Specimens examined. –JAVA: 4 ♂, Malang, iii.1933 (*J. G. Betrem*); 4 ♂, Malang, iv.1933 (*J. G. Betrem*); ♂, Nongkodjadja, 3000 ft., 1.ii.1936 (*M. E. Walsh*).

KANGEAN ISLANDS: ♂, Gunong Tinggi, 400 m., ii.1936 (*M. E. Walsh*); 2 ♂, Tembajangan, ii.1936 (*M. E. Walsh*); ♀, Boejoetan, 50–100 m., ii.1936 (*M. E. Walsh*).

Timulla (*Trogaspidia*) *amans oryzae* Pagden.

Timulla (*Trogaspidia*) *oryzae* Pagden, 1934, *J. F.M.S. Mus.* **17** : 426–433, figs. 3–6, ♂♀.
Timulla (*Trogaspidia*) *oryzae* Mickel, 1935, *Trans. R. ent. Soc. Lond.* **83** : 236, ♂♀.

Holotype and Allotype. –♂♀, *in copula*, FEDERATED MALAY STATES: Perak, Simpang Lima, Alor Pongsu, Krian, 20.v.1930 (*H. T. Pagden*) in British Museum (Natural History).

I have compared the male genitalia of this and the preceding species and am convinced that *oryzae* must be considered as a subspecies of *amans*. There is no difference in the genitalia and the small differences pointed out by Mickel in his key are too slight to have specific significance.

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CONTENTS

PAGE
Phipps, John, M.Sc., D.I.C., F.R.E.S. The structure and maturation of the ovaries in British Acrididae (Orthoptera) . . . 233–247, 7 figs.

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THE STRUCTURE AND MATURATION OF THE OVARIES IN BRITISH ACRIDIDAE (ORTHOPTERA).

By JOHN PHIPPS, M.Sc., D.I.C.

Manuscript received 9th August, 1948.

(Read 7th September, 1949.)

With 7 Text-figures.

THE observations described in the present paper were made during the summer and autumn of 1947 at the Imperial College Field Station, Silwood Park, Berks., as part of a larger population study being carried out by Dr. O. W. Richards and Dr. N. Waloff.

The grasshoppers of the family ACRIDIDAE occurring at Silwood Park are *Omocestus viridulus* L., *Stenobothrus lineatus* Panzer, *Chorthippus parallelus* Zetterstedt, *Ch. bicolor* Charpentier and *Myrmeleotettix maculatus* Thunberg. In addition to these, specimens of *Chorthippus albomarginatus* (De Geer) and of *Gomphocerus rufus* (L.) were obtained from Brentwood, Essex, and from Box Hill, Surrey, respectively. A continuous supply of these two species was not available and it was not therefore possible to make investigations on seasonal changes.

MATURATION OF THE OVARIES.

The ovaries of the ACRIDIDAE are of the panoistic type, each ovariole consisting of a chain of eggs. The egg nearest to the oviduct, referred to for convenience as egg$_1$, is always the largest, except in some abnormal conditions mentioned below. The egg above this is referred to as egg$_2$.

In the newly-emerged adult egg$_1$ is not more than 1·5 mm. in length, and the whole ovary is white and transparent (fig. 1). As maturation proceeds, all the egg rudiments grow, but each grows faster than the one immediately above it, so the initial differences in size become more pronounced, and at the same time the whole ovariole increases in length. Egg$_1$ begins to show a yellow colour when it is about 3 mm. long, the other rudiments remaining white.

The fully-matured egg, the size of which varies considerably even within a species, is shed into the oviduct, and the follicle which had contained it immediately shrinks to less than half its former length (fig. 2). The empty follicle now degenerates further and during this process a yellow substance is laid down in the wall of the ovariole where it joins the oviduct. This structure, referred to below as a *corpus luteum*, indicates that ovulation has occurred (fig. 2). It appears to be renewed by successive ovulations, though it often persists where ovulation has apparently not occurred for some time, as in some parasitized individuals. In all species examined it was absent only in immature individuals and in those mature ones which were taken early in the season and which might be supposed not to have oviposited. It is less deeply coloured and so less conspicuous in *Chorthippus bicolor* than in the other species.

The *corpus luteum* forms, in fact, a ring at the junction of ovariole and oviduct, this fact being very clearly shown in specimens dissected during ovulation, when the egg can be seen passing through the yellow ring (fig. 3). It appears probable that it is associated with some process of degeneration occurring at this point. Evidence for this view is adduced below in the section on abnormalities.

When egg_1 is ovulated, egg_2 is usually about 3 mm. long, and is already yellow.

It appears probable that the eggs may be retained in the oviduct for only a few hours or for a day or more, probably depending on the presence of suitable conditions and of a site for oviposition. That this variation does occur was indicated by the fact that in some individuals large empty follicles were present, showing little progress in degeneration, but there were no eggs in the oviduct, while in others eggs were still present in the oviducts, though the empty follicles had almost disappeared.

NUMBERS OF OVARIOLES.

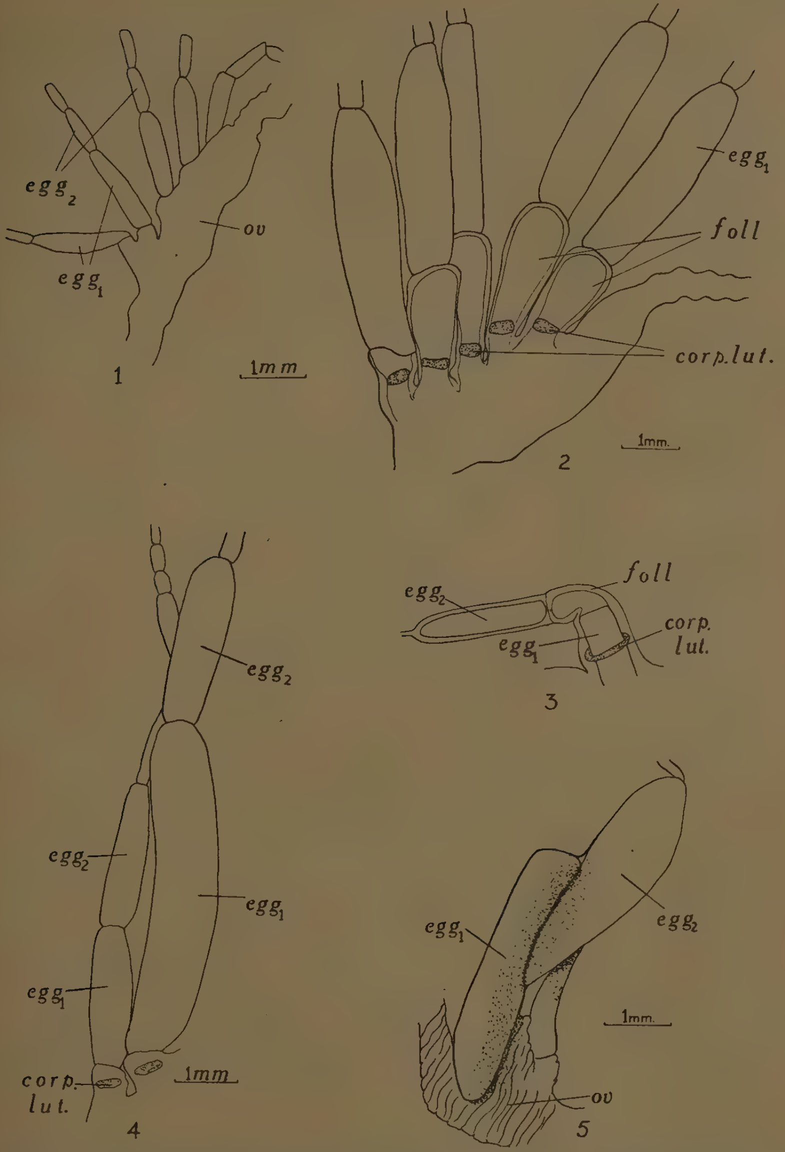
One of the purposes of the investigation was to determine whether egg-rudiments are continuously produced during the life of an individual, and to investigate possible change in the number of ovarioles. To this end observations were made on the numbers of ovarioles in the two ovaries (not necessarily the same in both) for nymphs, immature adults and adults which had become mature but had not ovulated. By a mature adult is meant one in which egg_1 is not smaller than the normal minimum size of egg_1 in a grasshopper which has ovulated.

It was found that in *O. viridulus*, *Ch. parallelus* and *G. rufus* (one specimen only) the number of ovarioles was constantly 5 & 5; in *S. lineatus* 4 & 4 and 3 & 3; in *Ch. bicolor* 8 & 8, 8 & 7, 7 & 7, 7 & 6, 6 & 6, 6 & 5, while in *M. maculatus* the number was constantly 3 & 3. The only specimens of *Ch. albomarginatus* examined had oviposited, but all these had 5 ovarioles in each ovary.

Rubtzov (1934), in his table showing the ovariole numbers for Siberian grasshoppers, did not note any variation in *S. lineatus*, but gives the ovariole number as 3 & 3. He notes, however, a variation of from 5 & 6 to 7 & 7 in *Ch. biguttulus*, which is closely allied to *Ch. bicolor*. Rubtzov also remarks that these variations were found between individuals from different places. In the present study variations occurred amongst individuals from the same place.

In all the five species which were continuously dissected some variation in ovariole number was noted at least amongst adults which had oviposited, including always some individuals in which the ovariole number was different on the two sides. This asymmetry never resulted in an excess of one side over the other of more than one ovariole.

In *O. viridulus*, out of a total of 87 females dissected, all had 5 ovarioles each side except four. Of these four one had 6 & 5, one 5 & 4, and two had 4 & 4.


egg$_2$
egg$_1$
ov
1
1mm
egg$_1$
foll
corp.lut.
1mm.
2
egg$_2$
egg$_2$
egg$_1$
egg$_1$
corp. lut.
1mm
4
foll
egg$_2$
egg$_1$
corp. lut.
3
egg$_1$
egg$_2$
1mm.
ov
5

FIGS. 1–5.—(1) Immature ovary of *Ch. parallelus*. (2) Ovary of recently-ovulated *Ch. parallelus* showing large empty follicles (*foll.*). (3) Portion of ovariole of *Ch. bicolor* showing egg passing through *corpus luteum*. *foll.*, empty portion of follicle. (4) One normal and one small ovariole from the ovary of *Ch. parallelus*. (5) Ovariole of parasitized *O. viridulus*, showing large egg$_2$ and deformed egg$_1$ bursting its follicle.

In *Chorthippus parallelus*, out of a total of 92 dissected, all had 5 ovarioles each side except four. Of these four, one had 6 & 5 and three had 5 & 4. In both *parallelus* and *viridulus* the individuals showing variation were found only during September and October.

In *Myrmeleotettix maculatus*, out of a total of 21 dissected, all had 3 ovarioles each side except four. Of these four, one had 2 each side and three had 3 & 2. Only one of the four was dissected in August, the other three in September.

In *Chorthippus bicolor* and in *Stenobothrus lineatus*, more variation was found. In *bicolor*, out of a total of 125 dissected, 45 had 7 & 7, 33 had 7 & 6, 24 had 6 & 6, and 12 had 8 & 7. In addition, the numbers 8 & 8, 6 & 5 and 5 & 5 occurred. The frequencies are symmetrically (but not normally) distributed about the mode 7 & 7. The numbers 6 & 5 and 5 & 5 were found only in and after September, though one of the 5 & 5 individuals had not oviposited.

In *S. lineatus*, out of 61 dissected, 31 had 4 & 4, 17 had 4 & 3, and 13 had 3 & 3 ovarioles. Here as many individuals with 3 & 3 ovarioles were found in August as in the succeeding months.

There is thus some little evidence that changes in ovariole number are seasonal in their occurrence. In particular it was noted that in *Ch. bicolor* those individuals with 7 & 7 ovarioles were always most frequent until November, when those with 7 & 6 became slightly more frequent. The difference, however, is not statistically significant. No fourth stage nymphs were taken after 19th August, so no new adults were added to the population after this date, and if there is in fact a tendency for the population to contain a larger proportion of individuals with a smaller number of ovarioles later in the season, this must be due to a higher death rate amongst those with more ovarioles. That it cannot be due to loss of ovarioles during the life of an individual is shown by the following observation. Towards the end of the season the egg rudiments begin to degenerate in the ovarioles, degeneration beginning at the top of the ovariole. Examples of this were found in *Ch. parallelus*, *M. maculatus*, *O. viridulus* and *S. lineatus*, and varied from the disappearance of a few rudiments from the top of the ovariole to the complete loss of all rudiments, leaving only the ovariole sheath. The earliest examples of this were met with on 25th September, and others during October, and there appears to be little doubt that it occurs only towards the end of the season, and perhaps towards the end of the life of the individual. No evidence was found to show that the empty ovariole sheath itself disappears, and from the date on which this rudiment degeneration was first noted, it obviously cannot be used to explain variations in ovariole number during August. On the other hand, it is reasonable to assume that females with more ovarioles, which produce on the average more eggs, will die sooner than those which produce less. It has been shown by Pospelov (1934) and by Hamilton (1936) that females of *Locusta migratoria* live longer if maturity is postponed or prevented by preventing pairing.

The causes of the observed variations in ovariole number are therefore uncertain. Rubtzov (1934) points out that in species in which the number of ovarioles is variable, the number increases in the cooler parts of the range, e.g. in Western Europe. The differences may therefore be genetic, but it is also possible that variations in food supply or in the microclimate may influence the number of ovarioles developed during the early part of nymphal life.

The changes in the ovaries which appear to be definitely of seasonal occurrence consist in the appearance of relatively undeveloped ovarioles. Differences in the rate of development of eggs in different ovarioles lead to the production of ovarioles in which egg$_1$ is much smaller than in the others, and may be no larger than egg$_2$ of the other ovarioles (fig. 4). The incidence of such " small " ovarioles throughout the season is shown in Table I, the number of small ovarioles being expressed as a percentage of the total number of ovarioles counted.

Table I.—*Showing Numbers of " Small " Ovarioles as a Percentage of Total in Semi-monthly Periods.*

	O. viridulus. Ovarioles.			*S. lineatus.* Ovarioles.			*Ch. parallelus.* Ovarioles.			*Ch. bicolor.* Ovarioles.			*M. maculatus.* Ovarioles.		
Period.	Total.	Small.	%.	Total.	Small.	%.	Total.	Small.	%.	Total.	Small.	%.	Total.	Small.	%
1 June–31 July	100	0	0	.	.	.	10	2	20	.	.	.	24	1	4·2
1 Aug.–15 Aug.	20	0	0	51	7	13·7	50	1	2	.	.	.	11	0	0
15 Aug.–31 Aug.	10	0	0	49	8	16·3	90	6	6·6	151	18	11·9	.	.	.
1 Sept.–15 Sept.	207	12	5·8	65	10	15·4	89	0	0	199	22	11·1	6	0	0
15 Sept.–30 Sept.	259	49	15·1	167	20	12·0	160	9	5·6	306	12	3·9	44	3	7·0
1 Oct.–15 Oct.	60	2	3·3	91	12	13·3	170	9	5·3	188	5	2·7	30	2	6·6
15 Oct.–31 Oct.	.	.	.	14	1	7·0	129	6	4·7	271	29	10·7	.	.	.
1 Nov.–8 Nov.	.	.	.	.	.	.	30	7	23·3	327	57	17·4	.	.	.

The percentage of small ovarioles thus reaches a maximum in the second half of August in *S. lineatus*, *Ch. bicolor* and *Ch. parallelus*, neglecting the 20 per cent. for June–July in the last species, which is based on only one individual. As food was very scarce in August, owing to the drying of grass, it appears probable, therefore, that the under-development of some ovarioles is due to competition between the ovarioles for the available food. In *O. viridulus* and *M. maculatus* maxima occur in the second half of September, near the end of the season, and in *Ch. parallelus* and in *Ch. bicolor* second maxima occur in late October and in November.

The occurrence of small ovarioles, of course, means that the number of eggs produced at one time is sometimes less than the total number of ovarioles. Variations in the number of eggs in the oviducts are discussed below.

NUMBERS OF EGG RUDIMENTS.

In counting egg rudiments preparatory to calculating the average numbers of rudiments per ovariole it was noted that in some individuals the number of rudiments in different ovarioles showed fairly wide differences. In most cases these differences did not occur, but in order to obtain a representative figure for those in which it did occur, the average number of rudiments per ovariole was calculated by counting the rudiments in as many as possible of the ovarioles in one ovary, and dividing by the number of ovarioles in which rudiments were counted. It was not always possible to count the rudiments in all the ovarioles, as these sometimes broke in manipulation, or abnormalities were sometimes present in some of them. In view of the fact that the rudiment number was usually constant, however, it is unlikely that very different results would have been obtained if all the ovarioles had been intact.

Table II shows the average number of rudiments per ovariole for nymphs, immature adults and mature adults. In all cases where a sufficient number of individuals was dissected, the standard deviation has been inserted, and the number of individuals is given in brackets.

Table II.—*Average Numbers of Rudiments per Ovariole. None of the Mature Adults included had Oviposited except those of* Ch. albomarginatus. *Numbers of Specimens Examined are given in Brackets.*

Species.	Average number of rudiments per ovariole.					
	Nymph.	σ.	Immature adult.	σ.	Mature adult.	σ.
O. viridulus	15·2 (7)	3·2	19·7 (7)	5·4	20·0 (10)	5·1
S. lineatus	.	.	23·0 (1)	.	20·4 (2)	.
Ch. parallelus	7·2 (2)	.	14·0 (11)	1·8	12·1 (9)	4·8
Ch. bicolor	14·3 (5)	3·4	18·6 (15)	3·9	20·0 (11)	4·4
Ch. albomarginatus	.	.	.	.	9–15 (6)	.
M. maculatus	18·3 (1)	.	20·6 (1)	.	17·0 (1)	.
G. rufus	.	.	.	.	16·8 (1)	.

The significance of the difference between nymph and immature adult and between immature adult and mature adult has been tested in all cases where a standard deviation for both was calculated. None of the differences is significant, indicating that new egg rudiments are not produced during these periods.

It will be noted that there is considerable variation in the number of rudiments per ovariole in each species. Rubtzov (1934) found that between different species the number of ovarioles and of egg rudiments per ovariole vary inversely. This was not found to hold in our grasshoppers, where *Ch. bicolor*, with the largest number of ovarioles, has also one of the highest figures for rudiments per ovariole.

The results of counts of egg rudiments in mature individuals are summarized in Table III. The season was divided into semi-monthly periods and the number of rudiments per ovariole calculated for each period as described above.

Table III.—*Number of Rudiments per Ovariole in Semi-monthly Periods for Five Species of* Acrididae.

Period.	*O. viridulus.*			*S. lineatus.*			*Ch. parallelus.*			*Ch. bicolor.*			*M. maculatus.*		
	A.	B.	C.	A.	B.	C.	A.	B.	C.	A.	B.	C.	A.	B.	C.
1–15 June	1	11·6	.	.	.	.	.	.	.	.	.	.	.	.	.
16–30 „	5	17·8	3·4	.	.	.	.	.	.	.	.	.	.	.	.
1–15 July	4	24·2	3·5	.	.	.	1	15·0	.	.	.	.	.	.	.
16–31 „	2	18·9	0·1	.	.	.	.	.	.	.	.	.	4	18·4	1·9
1–15 Aug.	2	16·2	0·8	7	19·1	2·4	5	12·3	1·2	.	.	.	2	17·0	.
16–31 „	.	.	.	7	19·3	3·3	8	10·5	1·4	11	21·1	3·7	.	.	.
1–15 Sept.	20	12·8	1·5	13	18·2	3·6	10	10·9	1·8	14	17·6	3·7	1	21·0	.
16–30 „	24	12·6	2·5	23	16·4	3·4	18	10·3	2·6	23	18·7	2·9	8	18·3	3·8
1–15 Oct.	5	11·7	1·8	12	14·1	2·3	15	9·2	1·9	15	17·9	2·6	5	16·9	2·7
16–31 „	.	.	.	2	13·5	0·5	13	10·1	1·9	21	17·5	2·6	.	.	.
1–8 Nov.	.	.	.	.	.	.	3	11·6	3·0	25	15·6	2·5	.	.	.

Column A. Number of individuals dissected.
„ B. Average number of rudiments per ovariole.
„ C. Standard deviation.

In many cases the amount of information is scanty, particularly at the beginning of the season, but tests of significance of the differences between means for different periods give some suggestive results.

In *Ch. parallelus* the average of 12·3 rudiments per ovariole for the period

1st–15th August was compared with each of the succeeding periods. The difference between the means for this period and for 1st–15th September and 15th–30th September were found not to be significant. The difference between the means for 1st–15th August and for 15th–30th August is just significant, corresponding to $P = 0{\cdot}05$, but in view of the small numbers involved and also of the fact that later counts showed a rise in rudiment number this figure is not regarded as very reliable. The difference between the means for 1st–15th August and 1st–15th October was found to be highly significant, however. This result strongly suggests that new rudiments are continuously produced during the first part of the season, and that no considerable reduction in rudiment number as a result of oviposition takes place. No individuals which had not oviposited were dissected after the first week in August. Late in the season, however, production of new rudiments becomes less or ceases, so that a fall in the number of rudiments results from continued oviposition. It has been mentioned above that towards the end of the season the rudiments begin to degenerate in the ovarioles, degeneration beginning at the top of the ovariole. The average number of rudiments for the second half of October, though larger than that for the first half of the month, does not differ from it significantly.

In *M. maculatus* and in *S. lineatus* the position is similar, a fall in the average rudiment number occurring in the first half of October.

O. viridulus presents a rather different picture from the above. The difference between rudiment numbers for 16th–30th June and 1st–15th July is significant, the number being higher in the latter period. This may mean that new rudiments are produced during the first part of adult life, without being counter-balanced by oviposition, but it is also possible that later emerged adults had more rudiments per ovariole, and that the average for the population was thereby raised. It is interesting to note that none of the individuals from which the figures for these two periods are compiled had, in fact, oviposited, the first individual with *corpora lutea* being dissected on 6th August. The difference between the means for 16th–30th June and 1st–15th September is highly significant, again showing a fall towards the end of the season, which came earlier for *viridulus* than for the other species. The differences between means for 1st–15th September and 1st–15th October, however, is not significant. This result is not easy to explain, though it may be that very little oviposition occurred during September.

In *Ch. bicolor* also a significant difference was found between the means for 16th–31st October and 1st–15th September, after which no further significant fall occurred until November. The difference between 16th–31st October and 1st–8th November is also significant, indicating a very rapid fall in rudiment number which could probably not be entirely accounted for by oviposition. It may be due to the degeneration of rudiments which has already been described. The fact that no fall occurred during September and October indicates that in this species, too, egg rudiments can be continuously produced, and it is thought that this process may have been hindered during August by the unusually hot, dry weather, resulting in a shortage of food.

It was hoped that dissections of caged grasshoppers, which had oviposited a known number of times, would throw further light on the question of the production of egg rudiments.

The number of pods laid was added to the average number of rudiments per ovariole when dissected, giving the total eggs produced by each ovariole. For two specimens of *O. viridulus* the figures were 22·6 and 18·0 respectively; for four specimens of *Ch. parallelus* 19·6, 19·5, 17·6 and 17·0 respectively; for three specimens of *S. lineatus* 26·0, 20·6 and 17·6 respectively, and for three specimens of *Ch. bicolor* 29·3, 28·6 and 13·6 respectively.

The results are inconclusive, since the figure obtained for "total eggs" is never greatly in excess of the sum of the average and standard deviation for the species as shown in Table II. In most cases, however, and particularly in *Ch. parallelus* and *Ch. bicolor*, it is nearer to this upper limit than to the average for the species, and when it is remembered that some of the grasshoppers considered were taken as adults in the field, and might have oviposited several times before they were caged, the figures obtained appear to be at least not incompatible with the assumption that new rudiments are produced during adult life. The method of dissection of caged individuals appears to be capable of providing a definite answer to this question, when sufficient results are available for strict statistical treatment.

These results as a whole afford strong evidence that in all the species considered egg rudiments are continuously produced in the adult, and that it is not possible to deduce the number of eggs which can be laid from a count of the rudiments in a newly-emerged adult.

This conclusion contradicts the results obtained by Rubtzov (1934), who estimated potential fertility from counts of rudiments in recently emerged adults. Rubtzov states that not more than half of the total number of eggs originally present was deposited. It is interesting in this connection to compare the number of rudiments per ovariole in four species of British grasshoppers with those given by Rubtzov (1934) for the same species from Siberia.

	Number of rudiments per ovariole in adults which have not oviposited.	
	Siberian.	British.
S. lineatus	25–29	16·8–24·5
O. viridulus	27–29	11·6–29·0
Ch. albomarginatus	17–20	9·2–15·6
Ch. parallelus	16–18	13·0–18·6

It is apparent that in British grasshoppers the range of variation is greater and the average smaller than in the Siberian grasshoppers. A further difference may be deduced from Berezhkov's (1929) and Maltsev's (1925) observations that *Ch. albomarginatus* produces on the average 15 egg pods per female. Rubtzov (1934) assumes that each pod will contain on the average 7 eggs, making the total number laid about 100. This assumption must mean that 30 per cent. of the ovarioles are "small," a much higher proportion than was found in any British species. It is unfortunate that in the present investigation only six specimens of *Ch. albomarginatus* were dissected, but these six gave 10 per cent. "small" ovarioles, a figure comparable with that obtained for the other species. This difference suggests that there must be more competition for food between the ovarioles in Siberian than in British grasshoppers, which must mean either that less food is available or that the rate of egg production is higher in Siberia. The differences are presumably correlated with the very different climatic conditions, and it is suggested that in Siberian grasshoppers the difference between rate of oviposition and rate of production of new egg rudiments is so great as to mask the latter process. It certainly appears that in dealing with British grasshoppers it is not possible to deduce potential fertility from a count of the rudiments per ovariole in young adults, but much more information is required as to the effect of climate and food supply on the rate of production of eggs and of new rudiments before the suggestion made here can be properly discussed.

A comparison of the course of events in *Ch. bicolor* and in the other species suggests that *Ch. bicolor* is less well adapted than the others to temperature conditions in Britain.

The summer of 1947 was unusually warm and dry, and was followed by a dry autumn with very little frost. *Ch. bicolor* was found fairly commonly until 8th November, only one day earlier than the latest date recorded by Lucas (1920), and did not show any decrease in rudiment number before November, except the temporary fall noted in August. It seems very probable that in a less favourable year the species would disappear much earlier and that the fall in rudiment number would not be observed. It is possible, of course, that under such conditions the production of new rudiments would cease earlier and the fall would occur sooner, but the fact remains that in 1947 the other species showed the fall in rudiment number and disappeared before *bicolor*. The conclusion suggested is that except in unusually warm summers *Ch. bicolor* does not mature early enough to pass the peak of reproductive activity before the weather becomes unfavourable for survival.

Further evidence for this view is obtained from a consideration of the time required for the maturation of the ovaries. The first adult *bicolor* was found on 1st July, and the first which had ovulated on 20th August. In the intervening period only 15 were dissected, but these were well distributed in time up to 7th August, after which no more were dissected until 20th August, when three were found with mature eggs and one with eggs in the oviduct. It appears, therefore, that about one month was required for maturation of the ovaries, compared with about one week for *Ch. parallelus*, derived from similar data. Further, nymphs of *Ch. bicolor* were last found in some numbers on 19th August, and the last adult which had not oviposited on 4th September. This interval is less than that in July, as might be expected if the species does, in fact, require warmer conditions for the attainment of maturity. It should be noted, however, that the first pod laid by the caged *bicolor* was deposited on 21st July, and some individuals oviposited less than three weeks after becoming adult. The conclusion as to the time required for maturation may, however, still be true of a wild population as a whole.

THE EGGS.

Records were kept of the numbers and sizes of eggs in the oviducts and in the ovarioles. The length of the egg was measured in each case with an eyepiece micrometer. Normally, little variation was found between eggs in the same individual, except, of course, where small ovarioles were present.

Some conclusions may be drawn from these records by comparing egg-sizes in mature adults which have not oviposited, mature adults which have recently ovulated (recognized by the presence of eggs in the oviduct or of large empty follicles) and mature adults which have not recently ovulated.

The average size of egg_1 in "not recently ovulated" grasshoppers was found to be nearer to the average size of an egg from the oviduct than to the size of egg_1 in "recently ovulated" individuals. This may indicate that a period of rather rapid growth follows ovulation, and is itself followed by a period of slower growth when the new egg_1 is almost ready. Except for definitely abnormal individuals, any grasshopper which has already oviposited gives the impression, on being opened, of being almost ready for ovulation. However, in view of the probability of the occurrence of a period of slower growth, and of the fact, noted in the section dealing with maturation, that the eggs may apparently be retained in the oviduct for some time, the period between successive ovipositions must be quite variable. Some evidence has been brought forward by Nefedov (1936) that definite oviposition periods occur in some grasshoppers in Siberia. The evidence is based on a calculation of the percentage of "mature" grasshoppers at different periods, and this percentage is shown to fall sharply at intervals. If such outbursts of oviposition do, in fact, occur, they are probably due to the occurrence of conditions suitable to oviposition and/or the completion of maturation, since the present study has provided evidence that the growth of eggs is essentially a continuous process.

Records of numbers of eggs in the oviducts show that in *Ch. parallelus* the average (for 12 individuals) is 9·2, for *O. viridulus* 8·5, for *S. lineatus* 6·4, for *Ch. bicolor* 12·2, and for *M. maculatus* 4·3.

The figures for average numbers of eggs in the oviducts, having regard to the number of ovarioles, show that *Ch. parallelus* is more efficient in egg production than the other species, since there is less difference between the average number of eggs produced at one time and the normal number of ovarioles. This result may be compared with the low percentage of "small" ovarioles found in *Ch. parallelus*.

THE EFFECTS OF PARASITISM.

Some of the grasshoppers dissected were found to be parasitized by larvae of the fly *Blaesoxipha*. The effects on the ovary of the presence of Calliphorid larvae are similar in all species. The number of larvae present is of considerable importance, since where only one larva was present, especially when it was small, the effect was slight. Usually two or three larvae were present, when the appearance of the ovary was quite characteristic.

In grasshoppers less affected each ovariole contains a normal number of rudiments. Egg_1 is fairly large, but very commonly consists of only a flattened shell. Egg_2 is frequently as large as egg_1, and may also be flattened (fig. 5). *Corpora lutea* are usually found where the ovariole joins the oviduct. It appears likely that the maturation of eggs continues in such individuals, but that the ripe egg is not passed into the oviduct, but degenerates in its follicle, while egg_2 continues to grow as it would if egg_1 were normally ovulated.

Loose eggs are commonly found floating in the body cavity. This condition may be produced as a result of the growth of egg_2 or higher eggs distending the follicle, which then bursts. The bursting may be helped by movements of the parasites. The presence of *corpora lutea* may be due to the degeneration of the eggs, or may only indicate that ovulation occurred before the parasite exerted the full effect.

In those individuals which have been more affected by the presence of parasites, the rudiments in some or all of the ovarioles degenerate. In such cases egg_1 and probably two or three more eggs are present, though some at least of them are flattened, but the upper ends of the ovarioles degenerate and the ovarioles are frequently entangled, probably by the movements of the parasites. In such cases it is often difficult to determine the number of ovarioles, and it is obvious that the presence of parasites has prevented further egg-production.

One specimen of *Ch. parallelus*, containing one parasite, showed no abnormalities, and appeared in fact to have ovulated shortly before dissection. One specimen of *Ch. bicolor*, also with one parasite, showed no abnormalities, and one of *O. viridulus*, with a large parasite, had fully-formed eggs in the ovarioles. The eggs, however, were slightly wrinkled and may have begun degenerating.

A number of grasshoppers were dissected in which flattened eggs were present in the ovarioles and in which egg_2 was larger than usual, but in which no parasites were found. It was at first assumed that these had been parasitized and had survived the emergence of parasites. This, however, seems unlikely in view of the number of such grasshoppers found. The total number of all species dissected from random collections which contained parasites was 14, and the number dissected with similar abnormalities but not containing parasites was the same. It would thus be necessary to assume that survival for some time after the emergence of one or more parasites was the rule rather than the exception, and this appears unlikely. More probably, when ripe eggs are not passed into the oviduct for any reason they degenerate, and eventually only flattened shells remain. At the same time egg_2 develops, so the appearance produced by the presence of parasites is due only to the failure of ovulation.

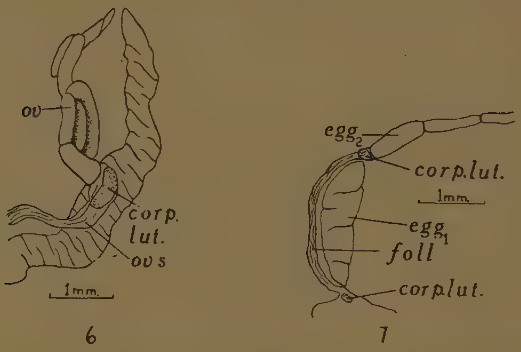
Evidence for this view was afforded by a specimen of *Ch. bicolor*, which contained only one small parasite, and was not obviously affected by its presence. When dissected it was ovulating, and it was noted that, while a number of eggs had already passed into the oviduct, others were still in the follicles, and two were tightly jammed in the neck of the follicle. These two were pulled through into the oviduct, and a groove was found round each where it had been held in the constriction. That the holding of the egg was not due to the dissection is shown by the fact that it was never noted in any other grasshoppers which were dissected while ovulating. The small size of the parasite also suggests that it prevents ovulation by means of a secretion which is passed into the body of the grasshopper. Somewhat similar appearances are noted by Rubtzov (1934) in grasshoppers parasitized by mites. Here, apparently, ovulation occurs, but the eggs degenerate in the oviducts, producing a condition similar to that described in the last paragraph on abnormalities below.

Grasshoppers may be attacked by *Blaesoxipha* either as nymphs or as adults. One fourth instar nymph of *Ch. parallelus* was parasitized, while, on the other hand, adults were dissected at the end of September, which contained quite small larvae.

ABNORMALITIES.

In the course of the dissections a number of abnormalities were noticed. Those resembling conditions produced by parasitism have been described above. Amongst the others a few appear to throw some light on normal function and may be worth consideration. Two of these showed the formation of a *corpus luteum* in an unusual position.

A specimen of *O. viridulus* dissected on 17th September had some flat eggs in the ovarioles, and in one ovariole a patch of yellow tissue, resembling a *corpus luteum*, at the lower end of the follicle of egg$_2$, i.e. between egg$_2$ and egg$_1$ (fig. 7). Egg$_1$ was an empty shell, which had burst out of its follicle, and egg$_2$ was much smaller than usual, and of rather irregular shape. It is probable that the occurrence of degeneration in the ovariole was the cause of the production of this *corpus luteum*.



FIGS. 6–7.—(6) Abnormal ovariole of *S. lineatus*, showing adhesion to the oviduct and *corpus luteum*. Below the adhesion the ovariole is empty (*ov. sheath*). (7) Abnormal ovariole of *O. viridulus*, showing flat egg$_1$ escaping from follicle (*foll.*) and *corpus luteum* below egg$_2$.

The other example was a specimen of *S. lineatus*, which appeared normal with the exception of one ovariole. This ovariole was attached, at a point near its upper end, to the upper end of the oviduct. Rudiments were present in the upper part of the ovariole, but below the point of adhesion to the oviduct the ovariole was completely "empty." At the point of adhesion a patch of yellow tissue was developed (fig. 6). This again appears to indicate that the *corpus luteum* is associated with degeneration.

A few examples were found in which the oviduct was swollen with some substance other than normal secretion (which coagulates immediately in water) or was quite hard and black. This was always associated with degenerating or flattened eggs, indicating that failure to ovulate results in the degeneration of the ripe eggs.

THE RELATION BETWEEN WEIGHT AND MATURITY.

The records of weights of grasshoppers were used to determine the possible existence of a relation between weight and nearness to oviposition. The results are given in Table IV. Eggs of slightly different lengths have been grouped in some cases, largely to obtain a sufficient number of weight readings for a given egg-size.

TABLE IV.—*Average Weights of Grasshoppers with Egg*$_1$ *of a given Length, with Numbers Dissected and Standard Deviations. Those with Eggs in the Oviduct are included together, irrespective of the Size of Egg*$_1$.

O. viridulus.

Egg length (mm.)	3·9	4·5–4·8	5·0	5·5–6·0	Eggs in oviduct
Number dissected	4	24	12	11	10
Average weight (mg.)	282·2	289·4	292·8	302·5	321·9
Standard deviation	33·3	41·5	49·0	32·5	59·0

Ch. parallelus.

Egg length (mm.)	3·3–4·0	4·5	5·0	5·2–6·0	Eggs in oviduct
Number dissected	3	17	18	16	14
Average weight (mg.)	185	189·5	211	210·4	209
Standard deviation	25·0	30·2	22·1	23·7	31·8

S. lineatus.

Egg length (mm.)	4·5–5·0	5·5	6·0–6·5	Eggs in oviduct
Number dissected	15	6	23	13
Average weight (mg.)	259·1	271·2	296	274
Standard deviation	30·7	37·0	35·0	39·7

Ch. bicolor.

Egg length (mm.)	3·0–4·0	4·5	5·0–5·5	Eggs in oviduct
Number dissected	11	23	29	16
Average weight (mg.)	212	228·4	238·6	248
Standard deviation	38·14	25·9	19·1	38·6

M. maculatus.

Egg length (mm.)	3·0–3·9	4·5	Eggs in oviduct
Number dissected	4	7	8
Average weight (mg.)	107·2	129	131·6
Standard deviation	5·1	6·2	11·5

It is clear that a steady increase in weight occurs with increase in egg-size. Individuals with eggs in the oviduct have a higher average weight than all the others except in *Ch. parallelus* and *S. lineatus*, where the average for those with eggs in the oviduct is less than the average for those with the largest eggs. This is probably because the size of ripe eggs varies considerably between different individuals of the same species, and in grouping together all those with eggs in the oviduct, some have been included with large eggs and some with small eggs, whereas in the other groups all those with large eggs are separated from those with small ones. The weight is therefore regarded as a measure of egg-size rather than of maturity. Because of this and because of the wide variation in weight of individuals with the same egg-size, the weight of one individual cannot be taken as an index of maturity. The average weight of a sufficiently large sample of a population, however, may be of some use in estimating the maturity of the population. In particular, it might be used to test the suggestion of Nefedov (1936) that definite periods of oviposition occur, as after such an outburst the average weight of the population should show a steep fall.

SUMMARY.

1. Specimens of *Omocestus viridulus*, *Stenobothrus lineatus*, *Chorthippus parallelus*, *Ch. bicolor* and *Myrmeleotettix maculatus* were collected at intervals throughout the summer, weighed and dissected. The condition of the ovaries was noted, eggs in the ovarioles and oviducts were measured and those from the oviducts weighed.

2. The process of maturation of the ovaries was followed, and it was noted that *corpora lutea* are formed after the eggs have passed into the oviduct, so that individuals which have oviposited can be recognized. The lowest egg in each ovariole is called egg_1.

3. The number of ovarioles in each species was counted and found to be variable in *Ch. bicolor* and *S. lineatus*, but fairly constant in the other species. It appears that the variation is possibly seasonal and some suggestions are made as to the causes of this.

4. Degeneration of egg rudiments in the ovarioles late in the season was noted.

5. The occurrence of relatively undeveloped ovarioles was observed, and it is suggested that this is due to competition for food between the ovarioles. The percentage is lowest in *Ch. parallelus*.

6. The number of egg rudiments per ovariole was calculated for each species for each semi-monthly period. No significant decrease occurs before the end of the season and it is concluded that rudiments are continuously produced during adult life, at least until late summer. Evidence on this point from caged grasshoppers is shown to be not incompatible with this conclusion.

7. The length of egg_1 was measured in nymphs, immature adults and mature adults of each species. In mature individuals which have not recently ovulated the average length of egg_1 was found to be nearer to that of an egg from the oviduct than to that of egg_1 in mature grasshoppers which have recently ovulated. It is concluded that ovulation is followed by a period of rapid growth of egg_1.

8. The average number of eggs in the oviduct was calculated and it was found that this differs least from the normal number of ovarioles in *Ch. parallelus*, which is concluded to be most efficient in egg production.

9. The effects on the ovary of parasitism by *Blaesoxipha* larvae were investigated. Evidence was obtained that ovulation is prevented and that developed eggs degenerate in the ovarioles.

10. Certain abnormalities were noted, two of which suggest that the formation of the *corpus luteum* is a result of a degenerative process.

11. The relation between weight and maturity was investigated. Weight was found to increase with increasing egg-size and it is suggested that the average weight of a population may be used in estimating the maturity of the population.

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Eu. 344

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CONTENTS

Butler, P. M., M.A., Ph.D. Observations on the biology of *Palorus ratzeburgi* Wissman, with comparative notes on Tenebrionidae in general (Coleoptera) . . . . . 249–273, 2 figs.

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OBSERVATIONS ON THE BIOLOGY OF *PALORUS RATZEBURGI* WISSMAN, WITH COMPARATIVE NOTES ON TENEBRIONIDAE IN GENERAL (COLEOPTERA).

By P. M. Butler, M.A., Ph.D.
(*Zoological Department, University of Manchester.*)

(Communicated by W. D. Hincks, M.P.S., F.R.E.S.)

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Introduction.

Palorus[1] Mulsant is placed in the subfamily Ulominae of the family Tenebrionidae. The subfamily contains a number of species associated with stored products, notably the species of *Tribolium* MacLeay, which have been the subject of many studies. *Palorus ratzeburgi* Wissman is frequently found in neglected corners of mills and granaries, where it is associated with *Calandra* (Kunike, 1934; O'Farrell and Butler, 1948), and it has also been reported on flour, bread and other cereal products. It is, however, of minor importance as a pest, and little is known of its life-history and habits. The fullest account of the life-history of a member of the genus is contained in a short paper by Zvierozomb-Zubovski (1923) on *P.* "*depressus*" (probably *P. subdepressus*). The genus has been reviewed by Blair (1930), and the larvae of the British species have recently been described by van Emden (1948).

The observations recorded in this paper were made during 1941–2 at University College, Exeter, in connection with the Standing Conference on Pest Infestation of Produce. The work was carried out under the general supervision of Dr. O. W. Richards. Material was supplied by the Pest Infestation Laboratory of the Department of Scientific and Industrial Research. In the limited time available it was considered advisable to extend the observations over as wide a field as possible, rather than to make an intensive study of any special aspect. Many of the conclusions reached should therefore be regarded as only tentative or approximate, but it is felt that the general picture obtained may be of some interest. Thanks are due to Dr. H. E. Hinton, Mr. W. D. Hincks and Mr. G. J. Kerrich for assistance with literature and for helpful suggestions.

The Egg.

Beetles did not oviposit in empty vessels, but did so readily in flour, when kept at temperatures of 25°C. or more. Eggs were obtained by sifting the flour, using a 60-wire mesh sieve (aperture 0·21 mm.); they measured about 0·45 mm. in length and 0·30 mm. in breadth. In order to facilitate the separation of eggs, the adults were kept in flour that had previously been passed through the sieve. The surface of the eggs was sticky and they were normally covered with particles of flour, or were found attached to the glass of the vessel in which the adults were kept.

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[1] Sometimes known by its synonym *Caenocarse* Thomson.

To determine the length of the incubation period, a culture was sifted at daily intervals, and each batch of eggs was kept in an empty watchglass and examined each day. At about 24° C. and a relative humidity of roughly 60 per cent., the eggs hatched in 7 to 10 days, the average for 90 eggs being 8 days. At about 27° C. the incubation period was 4 to 6 days, with an average for 75 eggs of 5·4 days.

The Larva.

Forty-two newly hatched larvae were placed separately in small flat glass dishes, the bottoms of which were covered with a thin layer of sifted flour (85 per cent. extraction). They were kept in an incubator at about 30° C. and 65 per cent. R.H., and examined daily for cast skins. Sixteen of these larvae completed their development: 3 passed through 6 instars, 7 through 7 instars, and 6 through 8 instars before reaching the pupal stage. Of the 26 that died, 14 did so in the second instar.

The duration of each instar showed considerable variation, as may be seen from the following figures, based on the 16 larvae whose development was completed:

Instar	1	2	3	4	5	6	7	Last	Total
Minimum (days)	1	5	4	4	3	4	4	7	30
Maximum (days)	3	13	8	10	15	9	9	14	59
Average	1·8	8·5	6·9	6·0	6·1	6·2	6·9	9·3	45·1

At about 24° C. the second instar averaged 10 days and the last instar 13 days.

A few rough observations were made on development at variable summer temperatures. About 200 fairly well-grown larvae, of approximately the same size, were divided into five groups of about 40. One group was kept at a temperature of 30° C. as a control, and the other groups were placed in the laboratory and in three greenhouses. The results are given in the accompanying table.

	Temperature (° C.).		Time to pupation (days).	
	Minimum.	Maximum.	Minimum.	Maximum.
Incubator	30	30	8	18
Stove greenhouse	18–22	26–31	22	40
Tomato greenhouse	11·5–19	Usually 21·5–27 (over 27 on 3 days)	30	50
Cool greenhouse	(normal range 12·5–21)		42	55
Laboratory	10	20·5 (over 25 on 3 days)	60	Over 75

It will be seen that the time of development in these buildings was several times as long as in the controls kept at 30° C. In unheated buildings in Britain larval development would take several months, and it is unlikely that more than one generation would be passed in a summer. Development would be favoured by the artificial heating of buildings, as, for instance, by milling machinery, or by the heating of grain.

The first instar larva is unpigmented and transparent, but in the second and subsequent instars the larvae are more strongly sclerotized except immediately after ecdysis. In each instar the head is large in proportion to the body at first, but the body lengthens and the head appears small towards the end of the instar. Shortly before ecdysis the larva becomes quiescent, and its body shortens. Ecdysis takes place by a splitting of the skin on the top of the head and the anterior part of the dorsal side of the body, the posterior end of the abdomen being the last part to be removed from the old skin. The first-instar larva is 1·7 mm. long.

Some measurements were made of the width of the head capsule in larvae of known age. Owing to the variation in the length of the larval stages, an increasing degree of overlap took place in the later instars. The largest larvae had head-widths of 0·48 mm. Head-widths measured by van Emden (1947) ranged from 0·35 to 0·54 mm.

Instar.	Head-width (mm.).
1 . . .	0·13–0·16
2 . . .	0·21–0·23
3 . . .	0·23–0·28
4 . . .	0·29–0·34 (approx.).
5 . . .	0·35–0·39 (approx.).

About three days before pupation at 30° C. the larva forms an oval chamber in the flour, usually near the glass of the tube. Inside this chamber it becomes quiescent, ceases to feed and takes on a curved, shortened form. Similar chambers were noticed among grains of wheat, the walls made of dust and excrement. Larvae will, however, pupate normally in empty tubes.

The larvae are negatively phototactic. In illuminated cultures in glass vessels there is a tendency for the pupal chambers to be formed on the shaded side. Fully developed larvae put into a long vertical tube of flour burrowed down to a maximum depth of 60 cm. and pupated deep in the flour.

Rough tests indicated that at about 25° C. and 60 per cent. R.H. larvae kept without food in empty tubes or in sand survived for 8–16 days. These tests were carried out on 30 half-grown larvae. In another experiment, 10 fully developed larvae were kept in empty tubes at 30° C. and 65 per cent. R.H.; they all pupated normally within 7 days, and all but two of them emerged as adults; the last adult died 15 days after the beginning of the experiment.

THE PUPA.

The pupal stage at 30° C. lasts from 4 to 7 days, the average for 16 individuals being 5·4 days. At 26° C. the length of the pupal stage is about 7 days, and at about 24° C. it is approximately 10 days. In a room with a temperature range of 13–33° C. pupae took about 18 days to emerge.

The pupa is at first quite colourless, but pigmentation of the eyes can be detected after a day or two and gradually deepens. Towards the end of the pupal stage sclerotization of the mandibles takes place, and about a day before emergence the whole pupa turns brown. In flour cultures the pupal stage is normally passed in the chamber constructed by the larva, and it is often possible to observe them through the glass of the vessel. The pupa is able to change its position in the chamber by a rapid flexion of the abdomen, and the same movement is shown if the pupa is touched.

The sexual difference in the terminal abdominal segment is very similar to that of *Tribolium* (Good, 1936). In the female, but not in the male, there is a pair of appendages anterior to the urogomphi. There appears to be a relatively high proportion of females; out of 219 pupae sexed from various cultures over a period of 7 months, 99 (45 per cent.) were male and 120 (55 per cent.) were female. A similar excess of females occurs in *Tribolium* (Good, 1936).

THE IMAGO.

When freshly emerged the imago is almost white, but pigmentation rapidly develops, and the full colour is attained in a few days. The imago is at first quiescent; after three days at 30° C. it begins to dig with its head and legs, and when about four days old it burrows its way out of the chamber. At room temperatures of 14·4–22·2° C., imagines remained in the pupal chamber for 5–11 days after emergence.

The length of the preoviposition period was studied by mating males and females of known age. They were sexed as pupae, and at a known period after emergence were placed together in small tubes of flour which was sifted at daily intervals to determine when the first eggs were laid. At 30° C. mature virgin females, when mated with mature males, begin to lay eggs one or two days after mating.

Temp.	Age in days when mated.		Number of cases.	Days to first egg.	Age in days when first eggs laid.	
	Female.	Male.			Female.	Male.
30° C. . .	0–5	26+	12	2–6	2–7 (av. 5)	..
	25–37	0	4	5–8	..	5–8 (av. 6)
	0–3	0–5	13	2–10	3–11 (av. 6)	2–11 (av. 7)
25° C. . .	4	Old	2	13	17	
	28+	1–5	3	12–20	..	15–25 (av. 19)
	0–4	0–6	12	13–39	13–39 (av. 21)	13–39 (av. 24)

The experiment showed that at 30° C. both sexes are mature in less than a week after emergence, but at 25° C. maturity is delayed to two or three weeks.

The imagines live for several months at least. One female of unknown age was isolated in April and kept at 25° C. until it died in the following November. Two other females lived at 30° C. from before September until May of the following year. Eleven females known to have emerged early in February were kept at 30° C. until the end of July, when they were still laying eggs.

Two females kept unmated for 86 and 109 days from emergence began to lay fertile eggs when mated with males aged 102 and 100 days respectively.

Copulation was observed frequently, and appears to take place several times in the life of the insect. Copulation lasts for about a minute.

The general behaviour of the adults is very similar to that of *Tribolium* as described by Park (1934) and Good (1936). They are negatively phototactic. They also appear to be negatively geotactic, as they tend to walk up an inclined plane in the dark When kept in glass dishes they show a marked tendency to try to climb up the sides of the dish, with the result that they fall on their backs. They cannot climb up clean glass, but can escape from dusty glass tubes. They have a tendency to get into small crevices. They feed while walking slowly over the surface of the flour, picking up pieces as they go and carrying them with the mouthparts. A beetle was seen to pick up a cast larval skin with its front legs and chew it with its mandibles, pushing it forward with its fore feet. To disagreeable olfactory stimuli or to a light touch with a needle on the head or antenna the beetle reacts by retreating a few steps and then setting off in a different direction. Strong stimuli induce a state of catalepsy which lasts for about a minute and cannot be prolonged by further stimulation. If a beetle falls on its back on a flat surface it cannot right itself; it moves its legs and antennae and twists its prothorax to one side, until one of the tarsi reaches an object in the neighbourhood. In one case a beetle was observed to spread its wings while struggling on its back; this was the only occasion in which spreading of the wings was seen. Flight was never observed. No exudation of scent was noticed, such as occurs in *Tribolium.*

Survival without food appears to depend upon temperature and humidity, but only a few rough experiments were made, the results of which are tabulated below:

Conditions of experiment.	Temp.	Approx. R.H.	Number of beetles.	Days survived.
Empty tubes	30° C.	65%	15	3–8
Closed vessel containing water	30° C.	100%	3	7–14
Empty tubes	25° C.	80%	10	8—more than 19
Sand	25° C.	80%	10	6—more than 19
Open vessel in lab.; expt. started May 21	Summer R.T.	Uncontrolled	7	18–28
Closed vessel containing water, in lab.; expt. started May 21	Summer R.T.	100%	10	18–56
Closed vessel containing water, in lab.; expt. started Nov. 24	Winter R.T.	100%	3	38–122

Low temperature and high humidity appear to favour survival without food.

In the last experiment, three beetles were kept in a glass staining-jar in which was placed a tube of water. The jar was kept in the laboratory through the winter, and the beetles lived for 38, 77 and 122 days respectively. The temperature fell to 4° C. for short periods, but it did not drop below 10° C. for more than two days at a time. It was noticed that the beetles became motionless when cooled to 10° C.

RATE OF OVIPOSITION.

A number of females, mated soon after emergence, were kept separately in tubes containing sifted 85 per cent. extraction flour. The flour was resifted every two days to determine the number of eggs produced. Ten insects treated in this way were found to lay eggs for between 164 and 170 days, when the experiment was discontinued. The temperature was maintained at 29·5–30·5° C., and the relative humidity averaged 80 per cent., though varying from 68 to 84 per cent.

The number of eggs produced per two-day period rose rapidly for 8 or 10 days from the appearance of the first egg, and after remaining at a high maximum level it showed a tendency to fall off. In continuously mated insects the greatest rate of oviposition was found during the period 20–60 days from the appearance of the first egg. The average daily rates for five pairs during this period, and also during the period 115–155 days, were as follows :

Female No.	Average daily egg yield.	
	20–60 days.	115–155 days.
1	3·1	3·1
2	3·8	4·1
3	3·9	2·7
4	3·9	4·1
5	5·3	3·9

A series of five females at least six months old (exact age unknown), kept under the same conditions as the younger series, showed daily averages of 1·2, 1·2, 1·7, 2·1 and 2·5 eggs respectively over a 28-day period.

The number of eggs laid by each beetle during successive two-day periods showed considerable fluctuation. The highest yield in two days was 14 eggs, in one instance ; 13 eggs were recorded three times, and 12 eggs eleven times.

In a parallel series of five (6–10) the males were removed immediately egg-production had begun. The changes in the rate of oviposition are shown in the following table :

Female No.	Average daily egg-yield.			
	6–20 days.	30–44 days.	100–120 days.	After male added. 128–166 days.
6	4·0	1·5	0·5	4·6
7	3·4	4·0	1·5	3·0
8	4·6	5·6	0·3	3·8
9	3·0	3·4	2·8	2·6
10	4·0	5·4	2·3	2·5

In three cases (6, 7 and 8) the egg production was reduced to a much lower level than in the continuously mated controls. When males were added after 120 days the egg production of the three females rose rapidly to a level comparable with that of the continuously mated females. Females 9 and 10, however, showed a smaller decline in the rate of oviposition, and the addition of males had no significant effect. It appears, therefore, that in some cases more than one copulation is necessary to maintain egg production, as in *Tribolium confusum* (Dick, 1937), but in others a single copulation is effective for over 120 days.

The effectiveness of a single copulation is shown by the following experiment: A young virgin female was mated, and copulation was observed to take place at once. The male was removed immediately, and the egg-production was followed by sifting at two-day intervals for 140 days. During this period only a slight decline was observed, from a rate of 4·2 eggs per day during the period 10–50 days to one of 3·5 eggs per day during the period 120–140 days. At the end of this time at least some of the eggs were fertile.

The rate of oviposition is much lower at 25° C. than at 30° C. Thirteen females that had been kept at 30° C. were placed in an incubator at 25° C. During the previous 20 days at 30° C. they laid an average of 32 eggs per day; from the 6th to the 19th day after the fall of temperature the average per day was 6·5. Not all the beetles were affected equally; two ceased to lay altogether, while at the other extreme two continued to lay at two-thirds of the former rate. Some typical examples are given below:

Average number of eggs per day.		
20 days at 30° C.	6–19 days after fall of temp. to 25° C.	Ratio.
2·4	1·6	0·67
3·6	1·6	0·44
2·6	0·4	0·14
2·8	0·1	0·05
4·2	0·1	0·02
3·2	0·0	0·00
Average of 13 *cases :*		
2·5	0·5	0·20

The lower temperature limit for oviposition would thus appear to be not much below 25° C.

A few observations were made at room temperatures. Two young females that had laid from two to four eggs a day at 30° C. were kept in the laboratory from March 19th till June 2nd, at a temperature range of 10–20·5° C. During this period one beetle laid one egg and the other laid three eggs. They were then returned to 30° C., and after four days oviposition began and rapidly rose to a level of 5 to 7 eggs per two-day period. A similar experiment was carried out on seven young females in a greenhouse in which the minimum temperature ranged from 11·5–14° C. and the maximum temperature from 19·5–28·5° C. At 30° C. the seven females produced an average of 27 eggs a day; during the first eight days in the greenhouse they laid altogether only 34 eggs; after this, oviposition almost ceased, only six eggs being laid in the next 48 days.

The production of eggs is reduced if the females are kept in flour of low moisture content. Five females, whose oviposition rates in flour at 30° C. and 80 per cent. R.H. ranged from 3·0 to 5·4 eggs per day, were placed in flour that had been kept at 30° C. in a desiccator over magnesium chloride (32 per cent. R.H.). The beetles were kept in the desiccator and the flour was sifted every two or three days for eggs. They laid from 1·3 to 2·6 eggs per day. They were then returned to flour at 80 per cent. R.H. for about 14 days, and the experiment was repeated, using anhydrous calcium chloride (13 per cent. R.H.). During 14 days over calcium chloride the average oviposition rate was 0·6 to 1·1 eggs per day.

DEVELOPMENT IN VARIOUS FOOD MATERIALS.

The food materials were placed in small glass vials, one inch in diameter, the vials being filled to a depth of about half an inch. To each vial was added a known number (15 to 25) of eggs not more than two days old, and the vials were kept in an incubator at 30° C. The contents of each vial were emptied out on a tray about every five days, and the living larvae or pupae counted. Owing to the difficulty of finding very small larvae, the first counts were in most cases made 15–20 days after the beginning of the experiment. Pupae were kept till they emerged, and the probable date of pupation was estimated from the date of emergence. Supposing the eggs to be on the average one day old, and the egg stage to last about five days, it was possible to estimate the length of larval development. The results for food materials in which development was completed are listed below :

Food material.	Percentage pupating.	Estimated larval life (days).
Wheat :		
Grains	24	32–44
" Bemax "	55	22–26
85% flour	50	24–29
" Coarse siftings "	58	21–33
White flour	42	24–37
" Old flour "	20	26–41
Broken grains	24	26–32
Macaroni	10	29–32
Semolina	33	34–56
Oats : rolled	50	25–48
Barley :		
Grains	18	35–37
Pearl	23	32–44
Rice :		
Polished	30	31–38
Ground	20	37–39
Flaked	20	57–92

Food material.	Percentage pupating.	Estimated larval life (days).
Maize :		
Damaged grains	20	36
Flaked	8	46
Flour	7	64–76
Split peas	5	48
Lentils	18	46–57
Sago	5	86
Tapioca :		
Powdered	5	44
Pearl	5	64
Dried milk	10	48–56
Sweet almonds	15	34–41
Linseed :		
Seeds	10	48–52
Cake	10	32–48
Dried apricots	5	56
Caraway seeds	3	60
Ginger : powdered	25	60–68

From the table it will be seen that the most rapid development and the best survival occurred in wheat products and in rolled oats. Among wheat products the best results were obtained in materials containing wheat germ : 85 per cent. extraction flour, " coarse siftings " (the fraction of 85 per cent. extraction flour that was retained by a 30-mesh sieve), and " Bemax " (a product containing a large proportion of wheat germ). In white flour the larval development took somewhat longer ; half the pupae were formed in 36 days as compared with 26 days in the 85 per cent. extraction flour. Mortality was higher and development relatively slow in " old flour," which had been used for a long time in a culture of *Palorus*, and contained large quantities of frass.

Development was completed on unselected wheat grains, but the newly emerged larvae are apparently unable to attack intact grains. Twenty eggs were added to intact wheat grains that had been examined individually under a microscope for signs of damage; no larvae were found alive after 14 days, and the grains had not been damaged. Repetition of the experiment gave the same result. On the other hand, larvae were able to attack wheat grains that showed very slight cracks in the region of the embryo ; they passed their earlier development inside the grains. When grown in wheat grains, the larvae nearly always removed the embryo ; in only one case was a grain attacked elsewhere than through the embryo. Damage to wheat grains closely resembled that done by other TENEBRIONIDAE, as described, for instance, for *Tribolium destructor* (Mathlein, 1943), *Eleodes hispilaris* (Wakeland, 1926), and various soil-living species in the Ukraine (Shchegolev, 1925).

The larvae were unable to feed on intact oat grains ; in one experiment, in which 20 eggs were added, two small larvae were alive 24 days later, but they died before the 30th day, and as there were no signs of damage to the grains they were presumably feeding on the dead bodies of other larvae. Intact maize grains were not attacked by young larvae, older larvae or adults, but if the grains had already been damaged by *Calandra* the larval development was completed, and adults laid eggs when kept in damaged maize grains. In haricot beans, one very small larva was still alive 22 days after 20 eggs had been added, but no damage to the beans was detected, and it was probably feeding either on dust or on the remains of the dead larvae.

There was some development in dried figs ; 20 eggs were added, and three living larvae were found after 22 days ; in 28 days two of these larvae were fairly large, but they were dead in 36 days. No development occurred in currants and dried apple. Under the comparatively high humidity in which the experiment was conducted, dried fruit tended to become moist and sticky, and this may have prevented the development of the larvae.

In tea, from 20 eggs added, one small larva was still alive 33 days later. In another experiment, two very small larvae survived for 13 days in tea. It seems probable that these larvae were feeding on the bodies of those that died.

Completely negative results were obtained when eggs were added to the following materials : Mustard, curry powder, cinnamon, ground coffee, cocoa powder, cloves, tobacco and maté tea. Large larvae survived 8 days in tobacco, 8 days in coffee and 17 days in cocoa, after which they pupated.

These experiments indicate a close resemblance between the nutritional requirements of *Palorus* and those of *Tribolium confusum* (Fraenkel and Blewitt, 1943) and *T. destructor* (Mathlein, 1943).

A few trials were made with natural materials. When 20 eggs were added to dead insects, one larva survived for more than 33 days and grew to a medium size ; it did not, however, complete its development. Medium-sized larvae grew when kept in a culture of dead insects, but the experiment was not completed owing to the development of moulds. In decayed wood from a tree trunk, several larvae survived 15 days and one of them 18 days, but all were very small. In soil, one very small larva was still alive 13 days after 20 eggs had been added. There was no development in broken cork.

Besides wheat flour, oviposition was observed when adults were kept in the following materials: slightly damaged wheat grains, "Bemax," macaroni, rolled oats, pearl barley, rice grains, ground rice, flaked rice, damaged maize grains, corn flour, almonds, and curry powder. Adults survived for over 50 days, but did not oviposit, in tapioca and sago. In intact wheat grains the death-rate of adults was high, but a small number of grains was attacked. There was no survival of adults in intact maize grains, intact dried peas, mustard, cinnamon, ground coffee, cocoa powder, tea, maté tea, or broken cork. In decayed wood five adults lived for over 13 days, but were all dead by the 18th day.

A Comparative Survey of Tenebrionid Life-histories.

In this section an attempt is made to review the literature on the life-histories of members of the Tenebrionidae, and to compare *Palorus ratzeburgi* with other members of the family.

Size of Egg.

The following papers give measurements or scale drawings of the eggs of various species: Zvierozomb-Zubovski, 1923 (*Palorus subdepressus*); Brindley, 1930 (*Tribolium confusum*); Chapman, 1919 (*T. confusum*); Fletcher and Ghosh, 1921 (*T. castaneum, Latheticus oryzae*); Mathlein, 1943 (*Tribolium destructor*); Morison, 1925 (*Gnathocerus cornutus*); Chopra, 1928 (*Alphitobius laevigatus*); Tischler, 1937 (*A. diaperinus*); Cotton and St. George, 1929 (*Tenebrio molitor, T. obscurus*); Oglobin and Kolobova, 1927 (*Asida lutosa, Pimelia subglobosa, Blaps halophila, B. lethifera, Opatrum sabulosum, Pedinus femoralis, Platyscelis gages, Crypticus quisquilius*); Kozlova, 1938 (*Opatrum triste*); Jack, 1914 (*Dasus aequale*); Coleman and Kunhikannan, 1918 (*D. hoffmannseggi*); Rodionov, 1927 (*D. pusillus*); Jack, 1918 (*Zophosis boiei, Psammodes scrobicularis, P. similis, Distretus amplipennis, Trachynotus geniculatus, Anomalipus plebeius*); Mail, 1937 (*Blapstinus substriatus*); Wade and St. George, 1923 (*Eleodes suturalis*); Gissler, 1878 (*E. gigantea*).

Although there is a rough correlation between the size of the egg in the Tenebrionidae and the size of the adult, the relative size of the egg differs considerably in different species. In *Gnathocerus* and *Alphitobius*, for example, the length of the egg is 20–25 per cent. of the length of the adult, while at the other extreme, in *Blaps* and *Eleodes*, they are relatively much smaller, only 6–9 per cent. of the length of the adult. The Ulominae all have relatively large eggs; in *Palorus ratzeburgi* the length of the egg is about 17 per cent. of the adult length, which compares closely with 18 per cent. for *Tribolium confusum*. *Opatrum* also has relatively large eggs, but in *Tenebrio* the eggs are small. Forms with large eggs have a shorter larval life than forms with small eggs; moreover, they lay their eggs at a slow rate over a long period of time, whereas forms with small eggs lay many in a short time (Dick, 1937).

Stickiness of Egg.

Stickiness of the surface of the eggs when first laid is a character very widespread in the family, and may be universal. It has been recorded for *Tribolium confusum* (Brindley, 1930), *T. castaneum* (Good, 1933), *T. destructor* (Mathlein, 1943; Reynolds, 1944), *Gnathocerus cornutus* (Morison, 1925), *Alphitobius diaperinus* (Tischler, 1937), *Tenebrio molitor* and *T. obscurus* (Cotton, 1927) and *Eleodes hispilaris* (Wakeland, 1926).

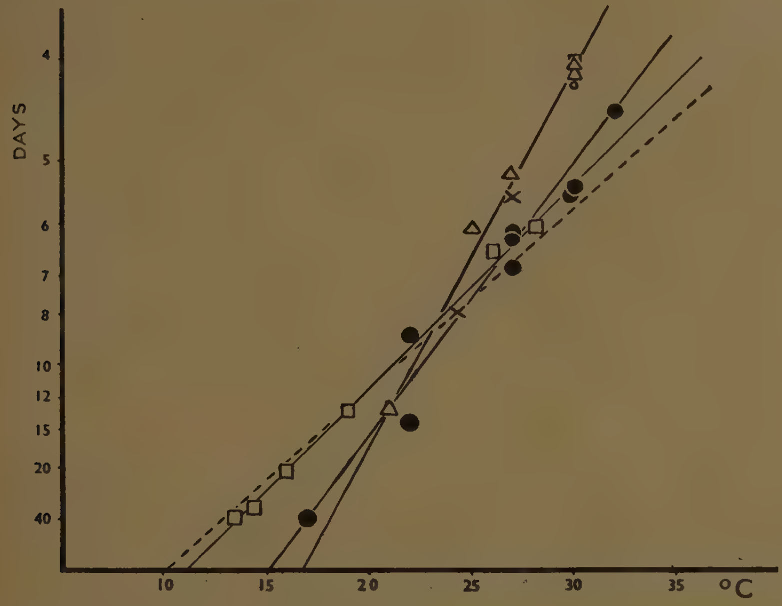

FIG. 1.—Reciprocal of incubation period plotted against temperature. From data published by various authors.

● *Tribolium confusum.* □ *T. destructor.* △ *T. castaneum.*
○ *Alphitobius diaperinus.* × *Palorus ratzeburgi.*

The dotted line represents *Tenebrio molitor* (points not indicated).

Incubation Period.

The incubation period becomes considerably reduced with rise of temperature, and many of the references in the literature are of limited value owing to the lack of temperature data. The following papers give the incubation periods of various species at recorded temperatures: Brindley, 1930 (*Tribolium confusum*); Good, 1933, 1936 (*T. confusum, T. castaneum*); Chapman and Baird, 1934 (*T. confusum*); Stanley, 1939 (*T. confusum*); Miller, 1944 (*T. confusum, T. castaneum*); Okuni, 1928 (*T. castaneum*); Mathlein, 1943 (*T. destructor*); Tischler, 1937 (*Alphitobius diaperinus*); Sanderson, 1910

(*Tenebrio molitor*); Cotton and St. George, 1929 (*T. molitor*, *T. obscurus*); Oglobin and Kolobova, 1927 (*Asida lutosa*, *Blaps halophila*, *B. lethifera*, *Opatrum sabulosum*, *Pedinus femoralis*, *Platyscelis gages*); Mail, 1937 (*Blapstinus substriatus*).

According to the formula of Blunck, as applied by Bodenheimer (1926), the rate of development varies as the "effective temperature," i.e. the difference between the recorded temperature and the minimum temperature for development. The reciprocal of the incubation time was therefore plotted against temperature, and for each species for which sufficient data had been obtained the points lay reasonably near a straight line (fig. 1). The minimum temperature at which development of the egg takes place is represented by the point where the line meets the temperature axis. It is about 10–11° C. in *Tenebrio molitor* and *Tribolium destructor*, probably somewhat higher (about 13° C.) in *Tenebrio obscurus*, about 15° C. in *Tribolium confusum*, and probably a little higher (about 17° C.) in *T. castaneum*. The slope of the line is greatest in *T. castaneum*, intermediate in *T. confusum* and least in *T. destructor* and in *Tenebrio*; at temperatures above 25° C., *T. castaneum* develops appreciably faster than the other species, and is thus able to make better use of short periods of high temperature. Data for *Palorus ratzeburgi* were obtained at only two temperatures, and are insufficient to deduce the minimum temperature for development; at 27° C., however, the rate of development resembles that of *T. castaneum*, and the difference between the rates of development at 27° and 24° C. would imply a high minimum temperature for development of the egg. *Alphitobius diaperinus* at 30° C. also develops rapidly.

Duration of the Pupal Stage.

The length of the pupal stage at known temperatures is recorded for the following species: *Tribolium confusum* (Brindley, 1930; Chapman and Baird, 1934; Park, 1935; Good, 1936; Miller, 1944); *T. castaneum* (Good, 1936; Miller, 1944); *T. destructor* (Mathlein, 1943); *Alphitobius diaperinus* (Tischler, 1937); *Tenebrio molitor* (Krogh, 1914; Sanderson, 1910; Payne, 1932; Cotton and St. George, 1929); *T. obscurus* (Cotton and St. George, 1929); *Eleodes suturalis* (Wade and St. George, 1923).

When these results are plotted in the same way as the data for the incubation period, a similar picture is obtained (fig. 2). The minimum temperature for development of the pupa is lower in *Tribolium destructor* and in *Tenebrio* (about 10–11° C.) than in *Tribolium confusum* and *T. castaneum* (about 18° C.). With increase of temperature the rate of development increases most rapidly in *T. castaneum*, and most slowly in *T. destructor* and *Tenebrio*, *T. confusum* being intermediate. *Palorus ratzeburgi* and *Alphitobius diaperinus* approach *T. castaneum* rather than *T. confusum*.

Duration of the Larval Stage.

The apparent similarity between the temperature relations of the incubation and pupal periods suggests that the larval stage would also be affected by temperature in the same way. The growth of the larva is, however, largely dependent on the rate of assimilation of food, and the duration of the larval period varies considerably with the food medium. This is shown by the work of Fraenkel and Blewitt (1943) on *Tribolium confusum*, as well as the experiments on *Palorus* described in the present paper. Good (1933, 1936), Park (1935), and Miller (1944) have also investigated the effect of nutrition on the development of the larvae of *Tribolium*. Each of these authors, however, worked at a single temperature, and comparison of their results is difficult owing to differences in food material and culture methods. Chapman and Baird (1934) give the length of larval life of *T. confusum* at three temperatures under similar conditions of feeding; at 22° C. the larval life averaged 60·6 days, as compared with 17·3 days at 32° C. This implies that development would cease at about 17° C. Menusan's (1936) figures for the time of development of *T. confusum* from hatching to the emergence of the imago, at 31·1° and 24·7° C. and various humidities, give by extrapolation a minimum temperature of development of 14–16° C. Mathlein (1943) gives the minimum larval life of *T. destructor* in rye flour at temperatures ranging from 30–31° C. to 16–17° C. By extrapolation from these results it would appear that the rate of development falls to zero at about 11° C. The minimum larval life occupied 70 days at 19–20° C. and 160 days at 16–17° C.; these figures agree with those of 76–96 days at 20° C. for *Embaphion muricatum* (Wade and Böving, 1921), and 110–130 days at 16° C. for *Eleodes suturalis* (Wade and St. George, 1923).

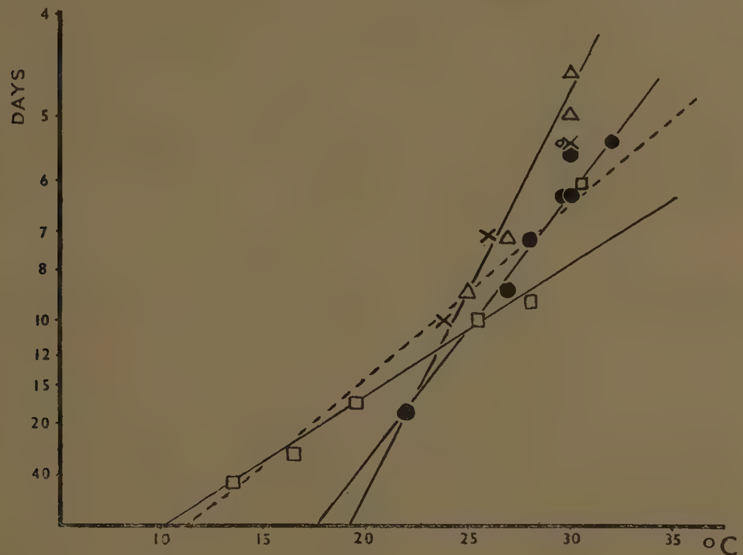

Fig. 2.—Reciprocal of pupation period plotted against temperature. From data published by various authors. Symbols as in fig. 1.

At high temperatures the larval life of *Tribolium castaneum* is longer than that of *T. confusum* under the same conditions. Miller (1944) compared the development of the two species in the same food materials, and found that under good feeding conditions the average larval life of *T. castaneum* at 30° C. and 75 per cent. R.H. was 18·5 days, as compared with 20 days for *T. confusum*; the minima were 16 and 17 days respectively. At 27° C., Good (1936) found a minimum larval life of 22 days in *T. castaneum* and 30 days in *T. confusum*.

Mathlein's (1943) results for *T. destructor* indicate a much slower larval development at high temperatures than in *T. confusum*; at 28° C. the minimum larval life was 31 days. This compares with Tischler's (1937) figure of 32–38 days for the larval period of *Alphitobius diaperinus* at 30° C., and the best result (26–30 days) obtained for *Palorus ratzeburgi* at 30° C. The slow development of these three species may well be due to suboptimal conditions of culture; in the experiments on *Palorus* there was a high death-rate even in the most suitable food materials.

That other factors than feeding may be at work is shown by the prolonged larval life of species of *Tenebrio* even at relatively high temperatures. Hein (1923) states that the shortest larval period of *T. molitor* occupied 9½ months at 30° C., and Lepesme (1944) gives 160–180 days as the length of larval life at 28° C. in *T. molitor*, and 90 days in *T. obscurus*.

Number of Larval Instars.

The TENEBRIONIDAE show considerable individual variation and specific difference in the number of larval instars. The normal number in the ULOMINAE is 6–8, but under conditions of drought or starvation the number can be increased to 11 or more. Thus the usual number in *Tribolium confusum* is 7 or 8 (Good, 1936), in *T. destructor* it is normally 6 (Mathlein, 1943), in *Latheticus oryzae* 6–9 (Barnes and Grove, 1916), in *Gnathocerus cornutus* 6 (Morison, 1925), in *Alphitobius diaperinus* 7 (Tischler, 1937), and in *Palorus ratzeburgi* 6 to 8. A similar number has been found in other subfamilies; thus *Dasus hoffmannseggi* has normally 7–9 (Coleman and Kunhikannan, 1918), though in dry conditions this can be increased to 13; *Eleodes suturalis* has 6 (Wade and St. George, 1923), and *Opatrum triste* has 7 (Kozlova, 1938). In *Eleodes hispilaris* and *E. sulcipennis* (Wakeland, 1926), 11 instars have been recorded however, and *Opatrum sabulosum* is stated by Oglobin and Kolobov (1927) to have 19 instars. It seems unlikely that so great a difference would exist between species in the same genus, and these data may have been obtained from insects bred under unfavourable conditions. However, in other species the number of instars seems always to be large; thus *Tenebrio molitor* has from 15 to 21 instars (median 17), according to Cotton (1927), while Hein (1920) gives the number of instars in this species as 10–16. In *T. obscurus* Cotton recorded 13–23 instars (median 15); Oglobin and Kolobova (1927) state that *Blaps halophila* has 12 instars and *Pedinus femoralis* has 11. A large number of instars is correlated with a prolonged larval life, either, as in *Tribolium*, the result of unfavourable conditions, or, as in *Tenebrio*, a normal character.

Relative Durations of the Instars.

The first instar is relatively short and the last one relatively long in *Palorus ratzeburgi*, *Tribolium confusum* (Brindley, 1930; Good, 1936; Park, 1935) and *T. castaneum* (Good, 1936), the intervening instars being about equal in length. In *Alphitobius diaperinus* (Tischler, 1937) the last instar is prolonged, but the first is similar to those that succeed it. The duration of each instar is affected by temperature, and results obtained at uncontrolled temperatures are not comparable, especially in those species that hibernate in the larval stage. It is likely that the first instar is usually the shortest in the TENEBRIONIDAE ; thus in *Tenebrio molitor* (Cotton and St. George, 1929), in June and July, when the temperature was very roughly 25–30° C., the first instar occupied 2–4 days and the second 7–16 days ; in *Eleodes suturalis* (Wade and St. George, 1923), at approximately 15·5° C. the first instar averaged 6 days and the subsequent instars between 10 and 27 days, though there was great variation ; in *E. hispilaris* (Wakeland, 1926) the first instar averaged 9·5 days, and the second 13·3 days ; in *Blapstinus substriatus* (Mail, 1937) the first instar lasted 7 days and the second 20 days ; in *Dasus hoffmannseggi* (Coleman and Kunhikannan, 1918) the first instar was the shortest in five life-histories tabulated ; in *Opatrum triste* (Kozlova, 1938) and *Blaps halophila* (Oglobin and Kolobova, 1927) the first instar is again the shortest. Exceedingly prolonged instars occur in *Tenebrio*, *Blaps*, *Eleodes* and other forms that pass the winter as larvae, presumably the result of a fall of temperature below the minimum for development.

Prepupal Larva and Pupal Cell.

A semi-dormant prepupal condition occurs in *Palorus ratzeburgi*, *P. subdepressus* (Zvierozomb-Zubovski, 1923), *Tribolium confusum* and *T. castaneum* (Good, 1933), *Alphitobius diaperinus* (Tischler, 1937), *Embaphion muricatum* (Wade and Böving, 1921), *Eleodes suturalis* (Wade and St. George, 1923) and species of *Tenebrio* (Cotton, 1927). It probably occurs in all species of the family (Oglobin and Kolobova, 1927). Except in *Tenebrio* and *Tribolium*, which pupate on the surface of the food material, the construction of an oval cell by the larva before pupation seems to be almost universal in the family. Among ULOMINAE this has been noticed in *Gnathocerus cornutus* (Morison, 1925) and *Alphitobius diaperinus* (Tischler, 1937), as well as in *Palorus ratzeburgi*. *Eleodes*, *Dasus*, *Opatrum*, *Blaps* and other terrestrial forms pupate in cells in the soil (Wade, 1921 ; Wade and St. George, 1923 ; Jack, 1913 ; 1914, 1928 ; Burns, 1929 ; Keuchenius, 1915 ; Oglobin and Kolobova, 1927). Other species excavate pupal chambers in decayed wood, e.g. *Pentaphyllus* and *Helops* (Perris, 1877), or in fungus, e.g. *Boletophagus* (Perris, 1877). In *Ceropria* and *Platydema* (Kemner, 1926) the larva spins a cocoon with a secretion from the mid-gut, and it is not impossible that a similar secretion is used to consolidate the lining of the pupal cell.

Preoviposition Period.

Few observations have been made on the preoviposition period in TENEBRIONIDAE. Mathlein (1943) gives 68–120 days as the preoviposition period of *Tribolium destructor* at 13–15° C., 21–29 days at 17–19° C., 12–22 days at 25–26° C., and 12–16 days at 28° C. From these figures it can be deduced that the preoviposition period would become infinitely long, i.e. no eggs would be laid at all, at about 11° C., which is also the minimum temperature at which the eggs develop. Reynolds (1944) studied the same species at 25° C., and found that when both sexes emerged at the same time the average length of the preoviposition period was 16 days, but was reduced to 12 days if the male was mature; it was influenced by the food material. Less is known about other species of *Tribolium*. Good (1936) gives records of ten matings of *T. confusum* at 27° C.; the beetles were mated 3–5 days after emergence, and the females began to oviposit at an average age of 8·2 days, the males at that time averaging 8·1 days. Some data are supplied by the same author for *T. castaneum*, in which eleven matings were made 1–11 days after emergence; the average age of the females when the first eggs were laid was 9·2 days and that of the males 10·8 days. Tischler (1937) says that *Alphitobius diaperinus* copulates a few days after its full colour is attained, a process which takes 3 days at 30°, but 20–25 days at 18–25° C. In *Palorus ratzeburgi* the first eggs are laid at an average age of 5–7 days at 30° C., and 19–24 days at 25° C.; this is a much greater retardation of maturity with fall of temperature than in *Tribolium destructor*, and implies that the minimum temperature for oviposition is appreciably higher, probably over 20° C.

A preoviposition period has been noticed in other subfamilies, but no observations have been made under conditions of constant temperature. In *Tenebrio* (Cotton and St. George, 1929) it lasts from 5 to 18 days at summer temperatures of about 27–30° C. *Eleodes suturalis*, according to Wade and St. George (1923), begins to lay eggs 20–22 days after emergence. In other species a much longer preoviposition period has been recorded; *Dasus depressus* in the East Indies (Keuchenius, 1915) becomes mature 6 or 7 months after emergence; *Zophosis boïei* (Jack, 1918) emerges in Rhodesia at the beginning of the wet season (November), but does not lay eggs till March or April; *Opatrum triste* in the Crimea (Kozlova, 1938) emerges in the late summer but does not oviposit till the following spring. In these cases it is unlikely that temperature is the only factor which delays oviposition.

Adult Longevity.

The majority of Tenebrionidae appear to be long-lived as adults, and go on laying eggs for a long time. Thus *Tribolium confusum* at 27° C. has an oviposition period of 136–325 days (Good, 1933), *T. destructor* at 25° C. 140–410 days (Reynolds, 1944), and *Gnathocerus cornutus* oviposited over a period of eight months at room temperature (Morison, 1925). An adult life of well over a year has been recorded for *Tribolium* (Good, 1936), *Blaps*, *Akis*, *Pimelia*, *Adesmia* (Labitte, 1916) and *Eleodes* (Wade and St. George, 1923). On the other hand, in *Tenebrio molitor* and *T. obscurus* the females live on the average for only 65 and 84·5 days respectively and have a correspondingly short oviposition period (Cotton, 1927; Dick, 1937). *Palorus* evidently resembles *Tribolium* in its long life and oviposition period.

Rate of Oviposition.

In *Tribolium confusum* the average number of eggs laid per day varies a great deal with the temperature, humidity, food and other factors. Dick (1937) obtained an average rate of 8·1 eggs per day at 27° C. and 65 per cent. R.H. during the period of maximum oviposition (24–32 days after emergence). Chapman and Baird (1934) obtained a rate of 10·7 eggs per day at 32° C., 6·6 at 27° C., and 1·9 at 22° C. Brindley (1930) obtained between 5 and 18 eggs per day at 29·7° C. (daily averages of 10 pairs ranged from 9 to 14). Under suboptimal conditions of culture much lower rates of oviposition are obtained (e.g. Park, 1935, 1936). In *Palorus ratzeburgi* the rate of oviposition was 3·1 to 5·3 eggs per day at 30° C. at the maximum period; these figures could no doubt be raised if special attention were paid to the conditions of culture, and it cannot be concluded that *Palorus* oviposits at a lower rate than *Tribolium confusum*. Reynolds (1944) obtained a rate of 1·6–4·4 eggs per day in *T. destructor* at 28° C.

In accordance with the shorter oviposition period, the species of *Tenebrio* lay eggs at a greater rate, as many as 62 eggs being laid in a day by a specimen of *T. obscurus* (Cotton, 1927). Great differences occur in *Tribolium* and *Palorus* between the number of eggs laid on successive days, and these differences appear to be accentuated in *Tenebrio*. A periodicity in oviposition has also been noticed in *Opatrum triste* (Kozlova, 1938); after each laying of usually 5–6 eggs, there is an interval of 1–2 days, which becomes prolonged to 4 or more days as the season advances. A similar periodicity probably occurs in *Eleodes suturalis*, which frequently lays 10–60 eggs together in one nest in the soil (Wade and St. George, 1923).

The lower temperature limit for oviposition is well above the lethal minimum temperature, and as a result the TENEBRIONIDAE lay eggs only in the summer in temperate climates, although in most species the adults survive the winter. According to Dick (1937) the lower limit for oviposition in *Tribolium confusum* is between 14° and 16° C. In *T. destructor* it is stated by Mathlein (1943) to be between 13° and 14° C. In *Palorus ratzeburgi* it seems to be somewhat higher, perhaps over 20° C.

Life-cycle in Relation to the Seasons.

Two main types of life-cycle are found in TENEBRIONIDAE living in temperate climates. In the ULOMINAE the winter is passed in the adult state, and oviposition is restricted to the warm part of the year; the larval development is completed during the summer months. *Palorus* clearly falls into this group; it oviposits only when the temperature approaches 25° C., and the growth of the larvae is very adversely affected by cool conditions. On the other hand, *Tenebrio* passes the winter as a larva which pupates in the spring; the adult lives for only a few months in the year. Among soil-living TENEBRIONIDAE, *Opatrum sabulosum* and *Dasus pusillus* overwinter as adults (Oglobin and Kolobova, 1927), while *Blaps*, *Pedinus*, *Platyscelis* and *Eleodes* hibernate as larvae, which have a slow rate of development. In the last four genera the adults survive the winter as well as the larvae, and they thus differ from *Tenebrio*, although according to Blaisdell (1909) *Eleodes clavicornis* is exceptional in that it probably lives only one season, and according to Wade and Böving (1921) over-wintering adults of *Embaphion muricatum* have a heavy mortality. *Eleodes hispilaris* takes two years to complete its development (Wakeland, 1925), probably owing to the brevity of the growing season. Adults which survive the winter may oviposit in two successive summers, e.g. *Blaps halophila* (Kolobova, 1925), or may delay oviposition until after hibernation, e.g. *Opatrum triste* (Kozlova, 1938). In tropical climates with a seasonal rainfall, the life-histories are similarly related to the dry season (Jack, 1918, 1928; Coleman and Kunhikannan, 1918). When conditions are suitable throughout the year, the life-cycle is apparently not related to the seasons, but breeding is continuous; this occurs probably with *Tribolium confusum* in the Gulf States (Good, 1933), and in continuously heated mills in cooler climates.

There are only a few scattered references to the effects of cold on adult TENEBRIONIDAE. Stark (1940) says that below 11° C. *Blaps halophila* and *B. lethifera* show scarcely any reaction to food. *Opatrum triste* (Kozlova, 1938) becomes torpid soon after the soil temperature has dropped below 10° C. *Palorus ratzeburgi* becomes torpid at about the same temperature. *Blapstinus substriatus* does not feed at 8° C. (Mail, 1937). According to Oglobin and Kolobova (1927) hibernation of various species found in the soil of the Russian steppes occurs when the temperature falls to 7° C. *Tribolium destructor* (Mathlein, 1943) becomes torpid at 5·5° C. Data on the lethal effects of low temperatures are equally scanty. A temperature of 7° C. kills all stages of *Tribolium confusum*, adults being more resistant than larvae (Nagel and Shepard, 1934). *T. destructor* can survive to a lower temperature, but is killed by 40 days' exposure to 3·5° C. (Mathlein, 1943). Temperatures below 10° C. are injurious to *Gnathocerus cornutus* (Morison, 1925). Larvae of *Tenebrio molitor* can survive for four months at a temperature of 0·5 to 5° C. (Mathlein, 1943). The ability to withstand winter cold must be one of the main factors controlling the distribution of TENEBRIONIDAE in temperate latitudes. The distribution of *Palorus ratzeburgi* in unheated parts of mills seems to indicate that this species can survive at a lower winter temperature than *Tribolium confusum*, but there is no direct evidence for this.

NATURAL HABITATS AND FEEDING HABITS IN THE TENEBRIONIDAE.

TENEBRIONIDAE are found in two main types of habitat; in and on the soil, and in association with decayed trees. Of the terrestrial forms, some are littoral, many prefer sandy situations, and terrestrial TENEBRIONIDAE form an important part of the fauna of deserts. Others are inhabitants of the soil of grassland areas, where a number of species are agricultural pests (Wakeland, 1921; Oglobin and Kolobova, 1927). Of the subfamilies found in forested areas, some inhabit the forest floor, the BOLETOPHAGINAE and most DIAPERINAE live in fungi growing on trees, and the ULOMINAE, TENEBRIONINAE and HELOPINAE are found mostly under the bark and in the decayed wood of trees. Except for *Blaps*, all the TENEBRIONIDAE associated with stored products are of arboreal origin. Species of *Palorus* have been found under the bark of trees in Europe (Champion, 1896; Seidlitz, 1898), and species of *Tribolium* occur in the same habitat in Europe and North America (Good, 1933, 1936; Leech, 1943). *Palorus*, *Tribolium* and *Latheticus* are frequently associated with wood-boring beetles, particularly BOSTRYCHIDAE (Andres, 1931; Beeson in Blair, 1930), and the related *Hypophloeus* is associated with SCOLYTIDAE (Peyerimhoff, 1919). *Alphitobius* is also found under bark (Seidlitz, 1898; Blair, 1928, 1935), and species of *Tenebrio* occur in decayed wood and similar situations (Leclercq, 1948).

The terrestrial TENEBRIONIDAE are predominantly vegetarian. Their larvae for the most part live in the surface layers of the soil and feed on roots, or gnaw the stems of plants just below the surface of the ground. Gilyarov (1927) concluded as a result of field studies that *Opatrum sabulosum* is primarily a humus-feeder in the larval state, but attacks plants to obtain food if the soil is poor, or moisture if the soil is dry.. There are many references in the literature to damage done to the roots or seedlings of agricultural crops; *Coniontis* (Vaile, 1913; Campbell, 1924), *Psammodes* (Jack, 1918) *Trachynotus* (Jack, 1913, 1918), *Distretus* (Jack, 1918), *Blaps* (Sakharov, 1939), *Eleodes* (Wade and St. George, 1923; Wakeland, 1926), *Embaphion* (Wade and Böving, 1921), *Opatrinus* (Dash, 1917), *Blapstinus* (Campbell, 1922, 1924; Mail, 1937), *Ulus* (Campbell, 1924), *Anomalipus* (Jack, 1918), *Dasus* (Jack, 1914, 1918, Keuchenius, 1915; Coleman and Kunhikannan, 1918; Sakharov, 1939; Hendrickx, 1943), *Opatrum* (de Bussy, 1913; Aoyama, 1920; Kozlova, 1938; Sakharov, 1939). The adults live on the surface of the ground and gnaw the stems of plants; in some cases they have been reported as eating leaves and buds. References to economic damage done are: *Zophosis* (Jack, 1918), *Blaps* (Vassiliev, 1913), *Eleodes* (Essig, 1913), *Blapstinus* (Mail, 1937), *Dasus* (Jack, 1918; Coleman and Kunhikannan, 1918; Anderson, 1924; Uichanco, 1928; Sakharov, 1939; Burns, 1929; Hendrickx, 1943), *Opatrum* (Aoyama, 1920, de Bussy, 1914; Soursac, 1924; Kozlova, 1938; Sakharov, 1939). Adults and larvae also damage seeds in the ground, particularly attacking the embryo and young sprout: *Zophosis* (Jack, 1918; Roubaud, 1916), *Homala* Roubaud, 1916), *Asida* (Wade, 1921), *Blaps* (Kolobova, 1925), *Eleodes* (Wade, 1921; Wade and St. George, 1923; Wakeland, 1926); *Embaphion* (Wade and Böving, 1921), *Platyscelis* (Shchegolev, 1925), *Pedinus* (Shchegolev, 1925; Shchelkanovtsev, 1927), *Blapstinus* (Wade, 1921), *Dasus* (Jack, 1914, 1918, 1919; Shchegolev, 1925), *Emyon* (Jack, 1919).

Some terrestrial species have also been recorded as feeding on dead or living animal matter: *Psammodes* larvae are very cannibalistic in confinement (Jack, 1918); *P. carbonarius* eats the eggs and even the nymphs of a locust (Cardoso, 1925); *Trachynotus griseus* is strongly attracted by dead insects but will not eat living insects (Jack, 1913); *T. geniculatus* is cannibalistic when kept in crowded conditions (Jack, 1928); *Dasus hoffmannseggi* eats dead specimens of the moth *Setomorpha* in packing-sheds in Java (Keuchenius, 1917); *Phaleria cadaverina* occurs in half-dried corpses of mammals on the shore (Seidlitz, 1898).

Among the arboreal forms, the BOLETOPHAGINAE and DIAPERINAE are fungus-feeders. One member of the DIAPERINAE occurs in stored products: *Alphitophagus bifasciatus*. According to Chittenden (1917) it occurs wild in fungus growing on trees, and develops in moist meal in which fermentation is taking place. The natural diet in the ULOMINAE and TENEBRIONINAE, to which most of the pests of stored products belong, is less clear. Eckstein (1934) failed to rear larvae of *Tenebrio molitor* on fresh timber, sawdust or shavings, and Park and Burrows (1942) were unable to maintain cultures of *Tribolium confusum* on wood-dust, although when 10 per cent. casein, 1 per cent. inorganic salts, 3 per cent. dextrose, and 5 per cent. yeast were added the insects survived and reproduced. The association of *Palorus*, *Latheticus* and *Tribolium* with wood-boring beetles, many of them "ambrosia beetles," may indicate that fungi play a part in the diet, but the survival of *Tribolium* and *Tenebrio* under very dry conditions would imply that fungi are not essential.

Fraenkel and Blewitt (1943) state that *Tribolium* can utilize cholesterol, sitosterol, or ergosterol, and thus could obtain its sterols from animal tissue, higher plants or fungi; carbohydrates are not necessary constituents of its diet. There are several records of ULOMINAE and TENEBRIONINAE feeding on animal tissue, usually dead or in a helpless state. *Tribolium castaneum* eats dead insects (Parker, 1916), the eggs of *Sitotroga cerealella* (Alden and Farlinger, 1931), the eggs and pupae of *Ephestia kuhniella* (Künike, 1939); *T. confusum* eats its own eggs and pupae in crowded cultures (Park, 1934); *T. destructor* completed its development on dead adults of *Ephestia kuhniella* (Mathlein, 1943); *T. madens* has been recorded as attacking Bibionid larvae in leaf-mould under a log (Leech, 1943); *Alphitobius diaperinus* will live on dead insects (Tischler, 1937); *Gnathocerus cornutus* eats the eggs, pupae and dead adults of *Ephestia kuhniella* (Morison, 1925); larvae of *Palorus ratzeburgi* increased in size when kept in dead insects; *Tenebrio molitor* larvae have been recorded as feeding on their own exuviae and on dead insects (Eckstein, 1934), and are sometimes found in the nests of birds, mammals and bees. *Palorus exilis*, *Diaclina* (*Alphitobius*) *rufotincta* and some species of *Tenebrio* have been found presumably feeding on the excrement of bats (Kemp and Chopra, 1924; Blair, 1936).

As a family the TENEBRIONIDAE appear to be basically omnivorous, though poorly adapted to a predatory habit. The terrestrial forms have become mainly herbivorous, and many of the arboreal forms have taken to a diet of fungi. The ULOMINAE and TENEBRIONINAE have probably retained the primitive omnivorous habit; they may well eat fungi on occasion, but there are no records of attempts to culture them on such a medium. They certainly cannot be regarded as specialized fungus-feeders like the BOLETOPHAGINAE and DIAPERINAE; perhaps they are adapted to live in dry wood where fungal growth is inhibited. The ability of *Tribolium*, *Palorus* and *Tenebrio* to survive and oviposit in dry conditions would support this view.

Their omnivorous habit and their ability to withstand dry conditions would provide a basis for the success of *Tenebrio* and the ULOMINAE in storage conditions. The winged arboreal TENEBRIONIDAE are often attracted by light to human habitations in warm climates at night, and economic species are sometimes taken at light; *Tribolium castaneum* (Blair, 1925), *Latheticus oryzae* (Blair, 1925; Andres, 1927), *Alphitobius laevigatus* (Blair, 1928), *A. diaperinus* (Blair, 1925) and *Tenebrio obscurus* (Blair, 1925). Alternatively the insects could get into stored grain from the timber used in the construction of native granaries. Perhaps a propensity to commensalism is shown by the occurrence of several species of *Tribolium* in the nests of bees and ants (Hinton, 1948) and of *Tenebrio* in the nests of birds and mammals (Leclercq, 1948). Once entry into food stores had been obtained, the spread of the species by commerce would become possible.

SUMMARY AND CONCLUSIONS.

A rapid survey of the life-history of *Palorus ratzeburgi* showed that this species closely resembles the species of *Tribolium*, which it also approaches in its general behaviour and dietetic requirements. The following differences were noticed:

1. The pupal stage is normally passed in a chamber in the food material, made by the larva; before pupation the larvae may burrow far below the surface of the food. *Tribolium* pupates on the surface of the food. The formation of a pupal chamber is widespread in the TENEBRIONIDAE, and it is probably a primitive character lost in *Tribolium*.

2. In some cases, but not in all, only one copulation is sufficient to maintain the production of eggs for a very long period. This has been noticed in *Tribolium destructor*, but in *T. confusum* more than one copulation is necessary.

3. The development of *P. ratzeburgi* is adapted to a relatively high temperature, and it probably resembles *T. castaneum* in this respect. The three species of *Tribolium* that have been investigated differ in the effect of temperature on the rate of development of the eggs and pupae, and probably of the larvae also.

4. The preoviposition period of *P. ratzeburgi* is much longer at 25° C. than at 30° C., and the rate of oviposition at the lower temperature is greatly reduced. Oviposition is much more adversely affected by low temperature than in *T. destructor*, and probably slightly more than in *T. confusum*.

5. The rates of larval development and of oviposition observed in experiments were lower in *P. ratzeburgi* than the best results obtained from *T. castaneum* and *T. confusum*, but comparable with those from *T. destructor*. It is possible that the lower results are due to suboptimal conditions of culture.

6. Species of *Tribolium* produce a characteristic odour, which was not observed in *Palorus*.

It is suggested that *Palorus*, like other ULOMINAE, is omnivorous in its natural habitat under the bark of trees and in decayed wood, and that the ULOMINAE are differentiated from other arboreal TENEBRIONIDAE like the DIAPERINAE in their ability to live in dry situations where fungal growth is inhibited.

The paper includes a review of the literature on life-histories and natural feeding habits in the family TENEBRIONIDAE.

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Vol. 100. Part 11. Pp. 275–289, 10 figs. 15th December, 1949

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Eu. 344

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CONTENTS

PAGE
HICKIN, N. E., Ph.D. Pupae of the British Trichoptera . . . . 275–289, 10 figs.

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PUPAE OF THE BRITISH TRICHOPTERA.

By N. E. Hickin, Ph.D.

Manuscript received 2nd December, 1948.

(Read 1st June, 1949.)

With 10 Text-figures.

The general morphology of the pupal stage of the British Trichoptera is described in this paper[1] and is a corollary to the work already published on the morphology of the larvae. Trichopterous pupae in the swimming phase (when they have cut their way out of the cocoon and are swimming in search of a suitable place for metamorphosis) constitute an important item in the food of fish, especially trout. Cast pupal skins on stones, or marginal vegetation, or floating on the surface of the water are often, however, the only indication to the biologist, fisherman or other investigator of a recent " hatch " of caddis fly. In this paper, therefore, special importance has been given to descriptions of those features of the pupae it is possible to examine in the cast skins. In addition, as many of these latter features as possible are incorporated into the key to the families.

In the work on the larvae referred to above, descriptions were made of the fully-grown larvae in the feeding condition (in those case-bearing types when the fore part is still able to emerge from the case in order to forage). This paper will thus commence with a description of the cocoon, the prepupal resting phase of the larva, and continue with descriptions of the pupa.

The material on which this paper is based has been obtained by the author during the rearing of Trichoptera from larvae to adults. Pupae have been preserved in the fluid advocated for this purpose by M. E. Mosely—one part of commercial formalin to nineteen parts of water—having first been placed in " collecting fluid " made up of two parts of 2 per cent. solution of formalin added to one part of 90 per cent. alcohol. Pupal skins were dehydrated in alcohol and mounted in Canada balsam.

I would like to place on record my deep sense of indebtedness to the late Martin E. Mosely for all the help and kindly criticism he tendered me during the last twelve years. This is my first paper on Trichoptera the manuscript and figures of which he has not painstakingly checked against the writings of previous authors or with material from the collections under his care.

All Trichoptera possess *pupae liberae*[1] and thus a general resemblance to the adult is shown by all pupae. The pupal integument is, for the most part, colourless and rather loosely envelops the formed imago lying beneath. The general shape of the pupa is, thus, that of the adult insect, and the sizes of the different parts of the pupa bear the same relation to each other as in the adult. There are, however, some features of the pupal integument of exceptional interest. The mandibles are large, well formed and functional, whereas those of the adult, on the other hand, are either absent or mere vestiges and are not functional. Moreover, the shape of the pupal mandibles is quite unlike that of the larval mandibles. The dorsal hook-bearing plates form a series of horny sclerites, variously shaped and situated, and used for gripping the sides of the case when emerging from it. Mandibles and dorsal hook-bearing plates are yellow, light brown or chestnut, and partly often black in colour in contrast to the third special feature of the pupal integument, the anal processes, which are of the same colour and texture as the general pupal integument. In some families of Trichoptera the pupal integument fits fairly closely the underlying genitalia, in other families two processes emerge more or less elongate and usually furnished with bristles. Because the pupal integument is almost transparent the underlying genitalia can almost always be seen, so that species determination can be made. This cannot, of course, be done with a cast skin.

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[1] The attention of readers of this paper is drawn to the paper by H. E. Hinton " On the Function, Origin and Classification of Pupae "(1949, *Proc. Trans. S. Lond. ent. nat. Hist. Soc.* **1947–1948**: 111–154). Hinton proposes the name *pupa dectica* for exarate pupae (*pupae liberae*) where functional mandibles exist, as in the Trichoptera. The development of pupal types in relation to their escape from the pupal cell is discussed.

THE COCOON.

All trichopterous pupae are protected by a cocoon In case-bearing larvae the cocoon is made from the larval case by blocking in various ways the front and rear openings. The cocoon thus made is anchored by secreted cement to a stone, water weed or some other submerged object. In some species the larva shortens the case before plugging, by cutting off one or both ends.

The plugging or sealing of the openings of the case is accomplished in diverse ways. In many species, e.g. *Limnophilus flavicornis* Fabricius, *Triaenodes bicolor* Curtis, a plug of cut pieces of water weed, tufts of alga or moss, or pieces of vegetable débris, is pulled in either at one end or at each end. This not only prevents the ingress of marauding carnivorous insects but often serves to hide the general shape of the case which might otherwise show up in its environment by its characteristic shape. Some species fill in the openings with a web of silk which is perforated in a characteristic manner, presumably in order to allow the passage of water through the cocoon for the gaseous exchange needed in respiration. This is correlated with the habit of the pupa of rhythmically undulating the abdomen to maintain a flow of water over the surface of the abdomen. Most often the pupal gratings are situated at the extreme ends of the case, but in some species they are fixed some way inside the case. In *Brachycentrus subnubilus* Curtis (fig. 1, C), the pupal grating consists of about eight small perforations in the centre of the disc. In *Sericostoma personatum* Spence the grating consists of an oblong slit (fig. 1, F), whereas in species of LIMNOPHILIDAE the grating consists of a number of perforations left in the weaving of algal filaments, fibres, etc. (fig. 1, G). In *Chaetopteryx villosa* Fabricius, the number of perforations is large, whereas in *Limnophilus rhombicus* L., it is small. Small stones are sometimes woven into the grating as in *Micropterna sequax* McLachlan (fig. 1, C and D), so that when the pupa cuts the grating away the stones come away with it. Species inhabiting fast running streams commonly plug the fore and hind end of the case with small pebbles, e.g. *Goëra pilosa* Fabricius (fig. 1, H), *Sericostoma personatum* Spence and *Odontocerum albicorne* Scopoli, but small pores allowing a flow of water through the case occur between the larger sand grains of which the cases are made. Pores such as those just described occur also in *Agapetus fuscipes* Curtis. In this species anterior and posterior openings occur on the ventral surface of the case and thus, before pupation when the case is fixed down on to a stone with silk, both openings of the case are closed. Thienemann reports that the terrestrial species, *Enoicyla pusilla* Burmeister, makes a simple membrane with no apertures. *Hydropsyche* constructs a pupal case by blocking in with small stones the shelter at the side of the net which is used during the larval stage. Completely free-living species such as *Rhyacophila* and *Philopotamus* construct cases of small stones fastened together with silk on to the side of a stone (fig. 1, J). In *Rhyacophila*, however, a characteristic cocoon is secreted within the

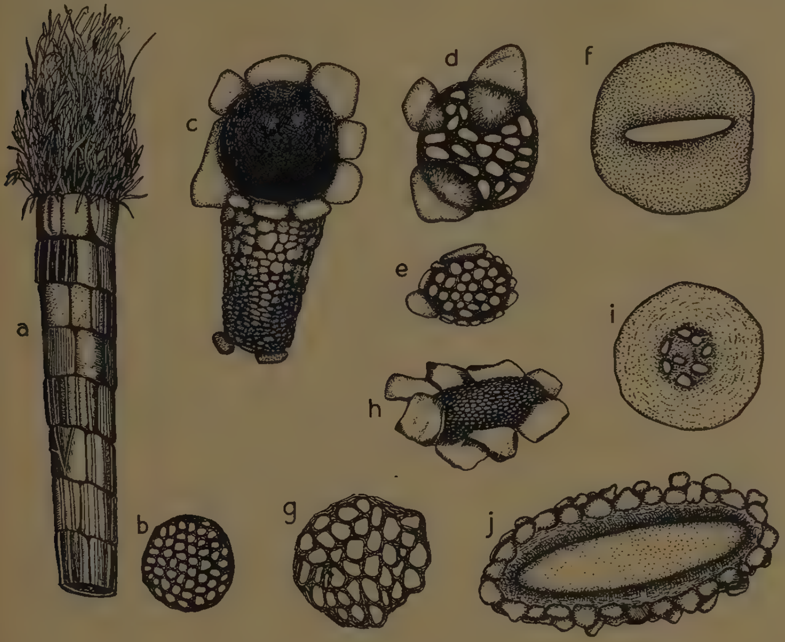


FIG. 1.—Types of case-plugging to form cocoon. A, *Phryganea varia* F., case with plug; B, *Phryganea varia* F., sieve membrane (posterior end); C, *Micropterna sequax* McLach., with sieve membrane cut off by pupa; D, *Micropterna sequax* McLach., anterior sieve membrane cut off by pupa; E, *Micropterna sequax* McLach., posterior sieve membrane; F, *Sericostoma personatum* Spence, anterior sieve membrane; G, *Limnophilus flavicornis* F., anterior sieve membrane; H, *Goëra pilosa* F., case with plug stones; I, *Brachycentrus subnubilus* Curt., anterior sieve membrane; J, *Rhyacophila dorsalis* Curt., case taken from stone, from below.

pupal case and entirely separate from it. This is membranous and tough, brownish in colour and semi-translucent.

In *Holocentropus* the cocoon is made by the secretion of a plentiful supply of silk to which is attached parts of decaying leaves of water plants.

In the HYDROPTILIDAE the pupal cocoon is made by filling the apertures of the larval case with a silken plug.

When the pupa emerges from the larva where a posterior sieve membrane is present, the larval skin breaks up into a number of pieces and is then kicked out of the pupal case through the pores in the membrane.

In *Rhyacophila*, however, where a membranous cocoon closely encompasses the pupa, the larval skin remains in various positions close to the pupa, the sclerotized parts being visible through the translucent cocoon.

PREPUPAL RESTING PHASE.

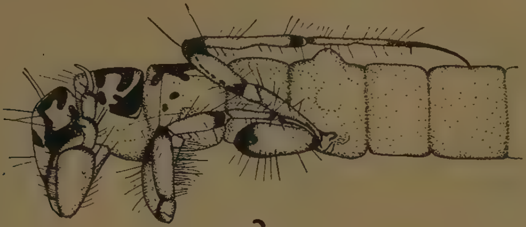
When the case has been plugged or otherwise completed certain changes take place in the larva. It becomes stiff, the head and abdomen losing their usual flexibility, and the intersegmental grooves of the abdomen become very indistinct. The legs then occupy positions characteristic of this phase only. In *Mystacides nigra* L. (fig. 2), the femur, tibia and tarsus of prothoracic legs are held up vertically, in the meso-legs coxa and trochanter are held downwards, the femur is held upwards and the tibia and tarsus backwards, whilst in the meta-legs the coxa points backwards, the trochanter and femur then extend forwards and towards the dorsal surface of the larva, the tibia and tarsus then turn backwards and follow the abdomen on the dorsal surface. (Lestage gives a figure of the larva of *Oecetis furva* where the legs are almost certainly in the position occupied in the prepupal resting phase.)

THE PUPA.

The head.—The head (fig. 5) is the same general shape as that of the adult but whereas in some organs, such as the eyes and antennae, the pupal integument follows closely the underlying adult shape, the mouth parts of the two stages are dissimilar. In the centre of the fronto-clypeal region of the head is a small conical projection. In *Mystacides* a transverse row of three equal projections occurs. Although instances have been given of adult Trichoptera feeding on nectar, such occurrences are extremely rare. The mouth parts are ill-adapted for such a purpose and can be considered for most practical purposes to be non-functional. (But Anker Nielsen has given an account of the species *Apatidea auricula* Forsslund which at high altitude in Norway pollinates *Ranunculus glacialis* whilst sucking nectar.) The mandibles of the pupae, on the other hand, have the important function of cutting the exit hole in the pupal case. In addition, the bristles of the labrum, assisted in some cases by the mandibles, serve to keep the anterior sieve membrane of the pupal case free from silt and debris, thus allowing an uninterrupted flow of water into the case. (This is related to the same function carried out by the anal processes or bristles on the posterior lobes of the abdomen in respect to the posterior membrane.) The bristles of the labrum have also been said to have secretory functions.

The eyes.—These are a prominent feature of the head of the pupa, and are the adult eyes covered by the thin, transparent pupal integument (fig. 5). In the fresh pupa they are light cream in colour but are black some time before emergence.

Antennae.—The pupal antennae follow closely the length, shape, number of segments, etc., of the underlying adult antennae. They are, however, loosely held down in a position different from that found in the adult. In the pupa, after skirting the eyes dorsally, they usually follow the anterior margin of the anterior wings. Thereafter, what occurs depends largely on the length of the antennae. In some species (fig. 4, B and C) the antennae are approximately equal in length or only slightly shorter than the wings, e.g. Sericostomatidae, Rhyacophilidae, Limnophilidae and Phryganeidae. Sometimes they are much shorter, e.g. Hydroptilidae, and in some cases they are extremely long and slender (fig. 4, A), being as long as twice or three times the length of the anterior wing, e.g., Leptoceridae. In many species of this family the tips of the antennae are wound round the posterior abdominal segments, and a pair of lappets bearing forwardly-directed bristles are situated on the 9th segment, e. g. *Mystacides azurea* (fig. 3, C). These keep the wound antennae in position and prevent them from slipping off and blocking the posterior sieve membrane of the pupal case. In *Leptocerus aterrimus* (fig. 3, B) lappets are



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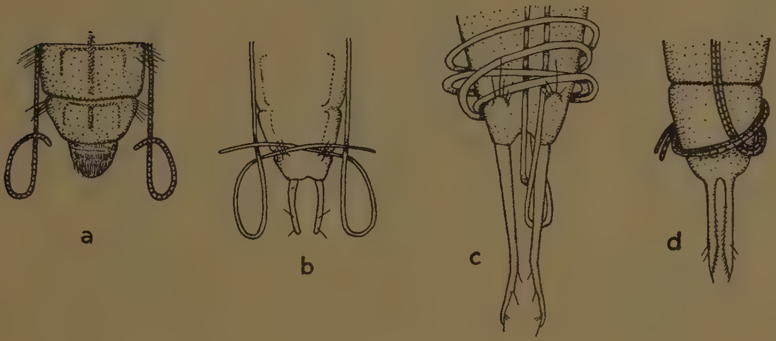

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Figs. 2–3.—(2) Prepupal resting phase of larva. *Mystacides nigra* L., lateral view. (3) Curling of pupal antennae. A, *Odontocerum albicorne* Scop.; B, *Leptocerus aterrimus* Steph.; C, *Mystacides azurea* L.; D, *Triaenodes bicolor* Curt.

present, but each antenna is loosely looped over on to the opposite side of the abdomen and not wound round the body. In *Triaenodes bicolor* (fig. 3, D) the antennae loosely adhere together and are wound round the abdomen in a clockwise direction for almost two complete loops.

Labrum.—This is a distinct, usually well-sclerotized part. It differs widely in shape in the different families, and there is variation also in the manner in which it projects from the head capsule. Bristles are an important feature of the labrum, not only in the placing but in the nature of the bristles themselves.

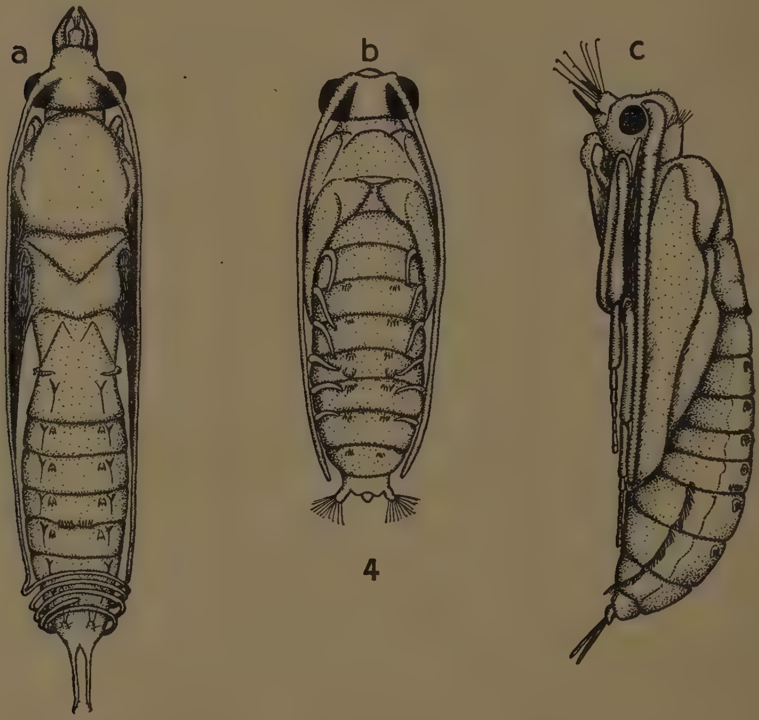

Fig. 4.—A, Dorsal view of pupa of *Mystacides azurea* L.; B, Dorsal view of pupa of *Plectrocnemia conspersa* Curt.; C, Lateral view of pupa of *Goëra pilosa* F. (Gills omitted).

In many pupae the labrum lies flat, in the same plane as the fronto-clypeus. In other pupae the labrum projects outwards from the head. In general the labrum is disc-like, wider at the base, but in some families it is narrower at the base—this is found in the case of the PHRYGANEIDAE (fig. 6, A) and in *Mystacides* (fig. 6, I), whilst in *Hydroptila occulta* (fig. 6, K) it is almost perfectly oval. Those species with the labrum wider at the base also show some thickening of this region and often a folding (*Odontocerum* (fig. 6, G) and *Rhyacophila* (fig.

6, J)) which sometimes gives a two-lobed effect. In *Lepidostoma hirtum* (fig. 6, E) the base is extended laterally.

A characteristic feature of the bristles of many of those species which construct the membranes in the openings of the cocoon is their long sturdy nature and the bending or hooking at the tip. In *Lepidostoma hirtum*, the tips of the bristles form a distinct loop. The function attributed to these bristles is the cleaning of the membranes of debris and silt in order to allow of the uninterrupted flow of water through the cocoon for gaseous exchange. The bristles are usually in fairly well defined groups, a pair of distal and a pair of proximal groups on each side. In *Limnophilus flavicornis* (fig. 6, B) the distal groups are hooked whilst, on the other hand, in *Lepidostoma hirtum* the proximal groups are hooked. In *Micropterna sequax* (fig. 6, D) neither group is hooked, although the bristles are long and strong, and project upwards from the suface of the labrum, but in *Leptocerus aterrimus* (fig. 6, H) and *Hydroptila occulta* (fig. 6, K) a single pair of bristles only is present, situated on the anterior margin, minute in the latter species.

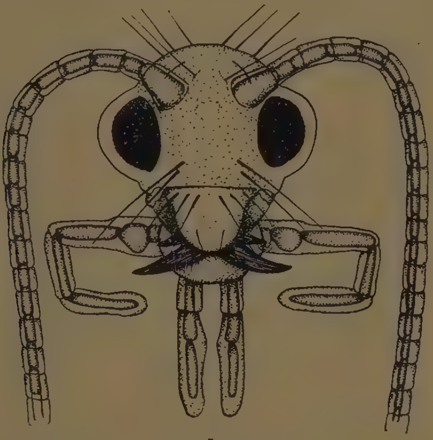

FIG. 5.—Head of pupa of *Rhyacophila dorsalis* Curt., from the front.

The mandibles.—The mandibles show a wide range of form, and many types are highly characteristic of their groups. They are well developed, robust, and well adapted to their function of sawing through the cocoon and thus releasing the pupa for its swim to the surface in order that metamorphosis into the aerial adult can take place. The mandibles are usually sickle-shaped with the base broad. Teeth are usually present and are of two distinct sizes. A few large teeth (nearly equalling in size the apex of the mandible) may be present, or the teeth may be small (they may be so small as scarcely to be distinguishable under a one-sixth inch microscope objective). In this species the inner edge of the mandible resembles a saw. In some species a combination of the two types of teeth may be present. A large number of species have two bristles on the outer convex side of the mandibles near the base. Articulation of the mandible with the head is by means of a spherical condyle on the base, usually between the centre and the outer edge, more rarely on the outer angle and the inner angle of the base of the mandible which makes contact with the sclerotized ring which surrounds the mouth parts (fig. 6, G).

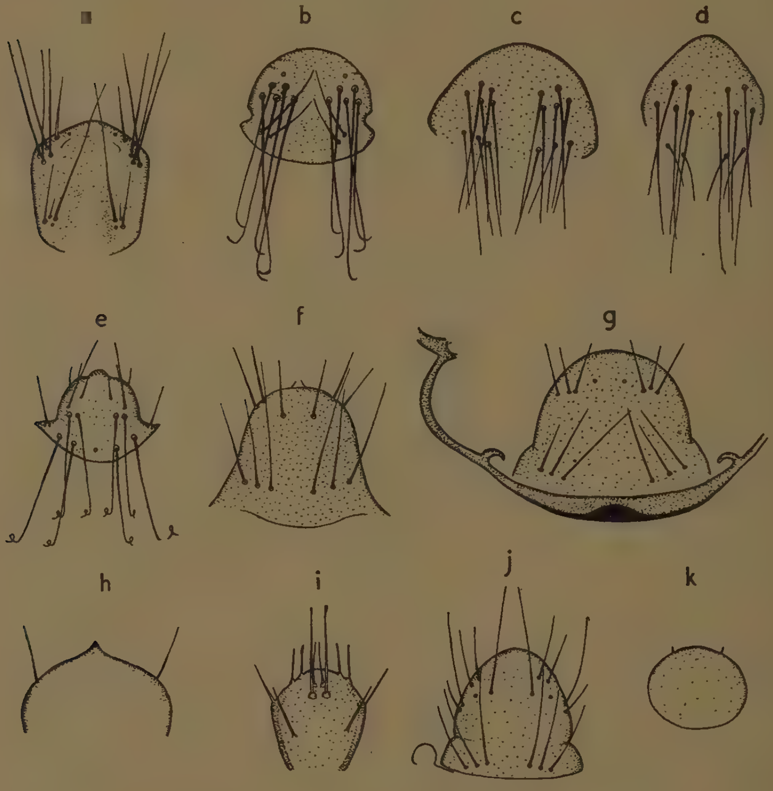

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FIG. 6.—Pupal labra. A, *Phryganea varia* F.; B, *Limnophilus flavicornis* F.; C, *Limnophilus extricatus* McLach.; D, *Micropterna sequax* McLach.; E, *Lepidostoma hirtum* F.; F, *Molanna angustata* Curt.; G, *Odontocerum albicorne* Scop.; H, *Leptocerus aterrimus* Steph.; I, *Mystacides azurea* L.; J, *Rhyacophila dorsalis* Curt.; K, *Hydroptila occulta* Eaton.

The mandibles of the PHRYGANEIDAE are characterized by having a slender inward-curving apical part with a stout base, and the bristles on the outer face are situated on a conical projection. The teeth on the inner edge are very numerous but can hardly be distinguished with a one-sixth inch objective

But Ulmer gives the mandibles of *Neuronia clathrata* as rudimentary. They are small and obtuse. Although I have twice searched the Staffordshire locality for this species I have not been fortunate enough to come across it. The mandibles of Rhyacophilidae, Philopotamidae and Hydropsychidae are all furnished with large teeth. In Rhyacophilidae they are asymmetrical, two teeth being present on the left mandible and three on the right. Figure 7 shows the range of shape shown in pupal mandibles.

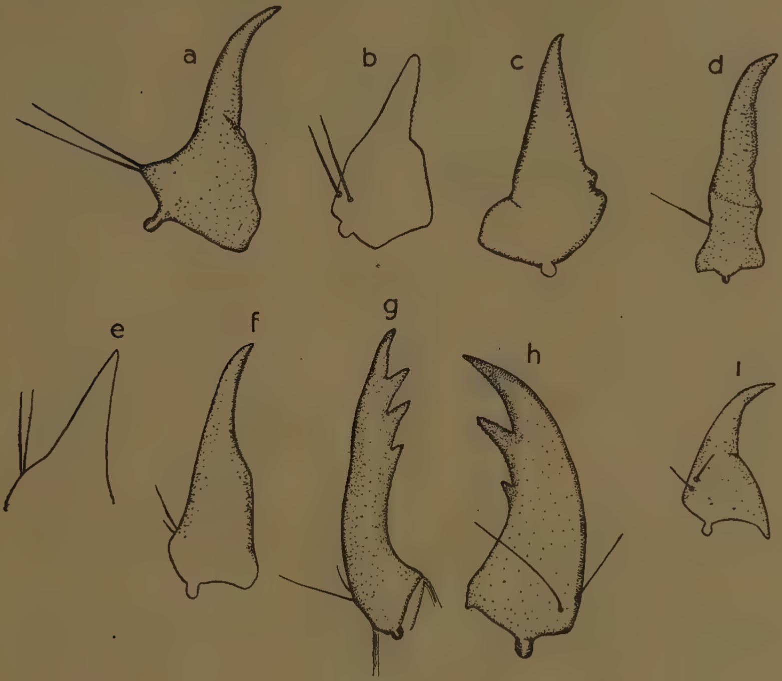

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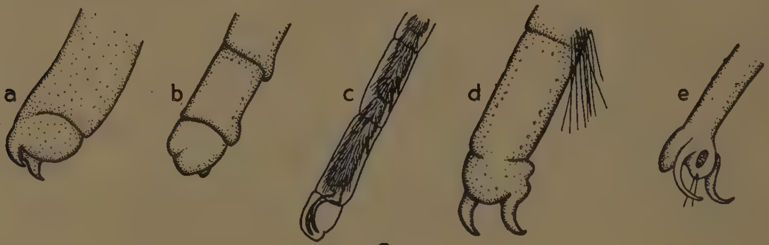
Fig. 7.—Pupal mandibles: A, *Phryganea varia* F.; B, *Limnophilus extricatus* McLach., C, *Goëra pilosa* F.; D, *Molanna angustata* Curt.; E, *Odontocerum albicorne* Scop.; F, *Leptocerus aterrimus* Steph.; G, *Philopotamus montanus* Don.; H, *Rhyacophila dorsalis* Curt.; I, *Hydroptila occulta* Eaton.

Maxillary palps.—These are well-defined in the pupa. Five segments are present in the maxilliary palp in the female in all families, but males of the family Phryganeidae have four-segmented palps, males of Limnophilidae and Sericostomatidae have three-segmented palps. Males of the remaining families have five-segmented maxillary palps similar to those of the females.

Labial palps.—These are always of three segments.

Wings.—These are held closely pressed to the pleural region of the thorax, and extend usually as far as the sixth segment, the tips of the fore wings almost meeting in the mid-ventral line. The wings are, of course, much smaller than the adult wings. The veins of the wing can often be made out after extraction of the wing from the pupal integument, but it would be unwise to rely on venation of the pupal wing as a determining characteristic. The wing venation cannot, however, be made out from the empty wing case.

Legs.—The legs of the pupa are free, the meso-legs entirely so, pro- and meta-legs have the coxa, trochanter and femur loosely adherent, but tibia and tarsus are free. The pupal integument follows fairly closely the shape of the adult legs and the segments correspond, but a separate segment is occupied by the tarsal claw and the number of segments of the tarsus is thus six. The tarsal claw segment shows a wide variation in shape, the pupal integument following to a greater or lesser degree the shape of the claws. In *Rhyacophila dorsalis* the claws are entirely separately ensheathed and a pore with a pair of bristles lies between them. In *Lepidostoma hirtum* the claws are separately ensheathed to the extent of about the distal two-thirds, whilst in *Phryganea varia* only about the distal one-third is separately ensheathed. In *Limnophilus flavicornis* only the tips of the claws are visible as a pair of blunt projections. The spurs of the adult are separately ensheathed by the pupal integument. When the pupa cuts its way out of the cocoon it swims actively to the surface, and thence to some object projecting from the surface of the water. The middle legs only are used for swimming and are well adapted for this purpose, as they are provided with a double fringe of hairs extending along the length of the tibia and tarsus. The "swimming fringes" are, however, often present on the other legs but are never so pronounced. Some species however, which live amongst wet moss, and thus do not require to swim, have the swimming fringe absent. This example of an important type of adaptation was given by Müller in 1879.



8

Fig. 8.—Tarsal claw of mesoleg of pupa. A, *Phryganea varia* F.; B, *Limnophilus flavicornis* F.; C, *Chaetopteryx villosa* F.; D, *Lepidostoma hirtum* F.; E, *Rhyacophila dorsalis* Curt.

The relation between the tarsal claws of the pupae and the habit of climbing from the water before emergence of the adult is easily seen.

Abdomen.—In shape, the abdomen of the pupa is generally similar to that of the adult but it is somewhat larger as no permanent retraction of the segments within each other has taken place at this stage. In addition, processes on the terminal segment often considerably extend the length. Nine segments are present. In those species where a lateral line is present in the larva, it is

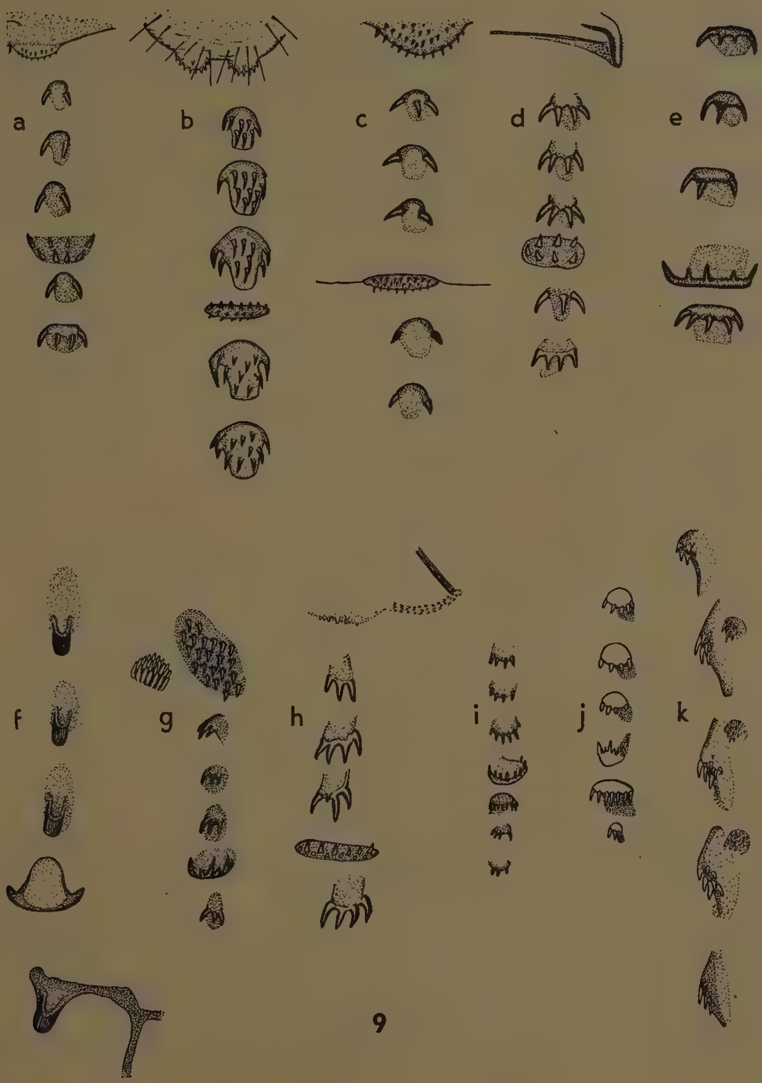


FIG. 9.—Hook-bearing plates of abdomen. A, *Limnophilus extricatus* McLach.; B, *Micropterna sequax* McLach.; C, *Goëra pilosa* F.; D, *Lepidostoma hirtum* F.; E, *Molanna angustata* Curt.; F, *Odontocerum albicorne* Scop.; G, *Leptocerus aterrimus* Steph.; H, *Mystacides azurea* L.; I, *Plectrocnemia conspersa* Curt.; J, *Philopotamus montanus* Don.; K, *Hydroptila occulta* Eaton.

present in the pupa also, but usually the hairs comprising it are longer and darker in colour than those in the larva. The lateral line in the pupa differs also from that of the larva by the posterior part curling under the posterior segments, and almost meeting at the mid-ventral line.

A number of skeletal rods are often visible in the pupal skin. These take the form of a series of umbrella ribs in each segment, often forked at the anterior end. They are quite hard, stiff and dark in colour and in some species some connection between the rods and the hook-bearing plate on the sixth segment is seen, e.g. *Odontocerum albicorne* (fig. 9, F). There are usually four rods in each segment, but in *Phryganea varia* two only occur in each segment. (One specimen only examined.)

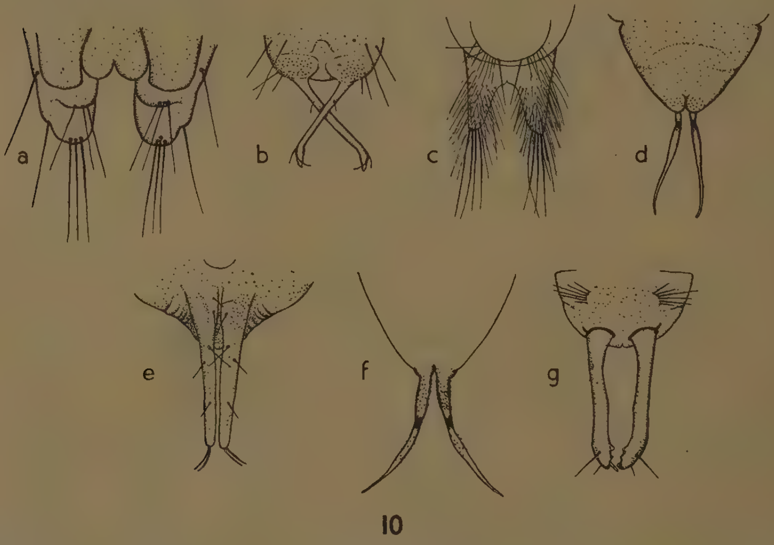


FIG. 10.—Anal processes of pupa. A, *Phryganea varia* F. ; B, *Micropterna sequax* McLach. ; C, *Goëra pilosa* F. ; D, *Lepidostoma hirtum* F. ; E, *Molanna angustata* Curt. ; F, *Odontocerum albicorne* Scop. ; G, *Leptocerus aterrimus* Steph.

A characteristic feature of the dorsal surface of the abdomen is the series of hook-bearing plates and other devices used for holding the inner surface of the pupal case. In Figure 9 the hook-bearing plates of a representative group of pupae are shown. Usually there is some modification of the dorsum of the first abdominal segment, but it is absent in those genera like *Rhyacophila* which do not move their abdomen when in the pupal case. It is thought that this device is for gripping the inner lining of the pupal case whilst the remainder of the abdomen is rhythmically undulated. At first sight it would appear that the abdominal hook-bearing plates are " gin-trap " mechanisms similar to those described by Hinton in certain beetle pupae. Closer observation, however, shows that the posterior plate on the fifth segment is thrown out of action (by the telescoping of the segment) when the anterior plates are forced downwards.

The hook-bearing plates thus serve only a locomotary function. There is a wide diversity in the form of this gripping device. In one genus, *Leptocerus*, it is not unlike, in general shape, the hook-bearing plates situated on the third segment onwards, except that it is much larger and contains many more hooks. Probably associated with the hook-bearing plates on the first abdominal segment in *Leptocerus* is a group of finger-like organs inclined towards the plate on each side. In *Limnophilus* the first abdominal segment extends backwards on the dorsal side into a pair of bulbous projections beset with short blunt spines. In *Mystacides* the bulbous projections are present to a lesser degree, but they are joined on the outside by a curved spinous bar which in turn is joined to a sclerotized bar pointing obliquely forwards. In *Lepidostoma* a narrow transverse band extends across the segment ending in the pleural region with a stirrup-shaped part, both arms of which are covered with small spines.

The second abdominal segment seems always to be devoid of hook-bearing plates, the series proper usually commencing on the third segment towards the anterior margin and repeated in the same place on the fourth, fifth and sixth segments. An additional plate on or near the posterior edge of the fifth segment is almost always present. The hook-bearing plates consist of sclerotized patches from which emerge a number of short hooks. The latter point backwards in the case of the anterior plates, and forwards in the case of the posterior plate on the fifth segment. The hook-bearing plates show a certain range of complexity, but it is almost a rule that the posterior plate on the fifth segment is larger and bears more hooks than the other plates.

In some genera the plate on the third segment may be absent, as in some species of *Limnophilus*. The series may terminate on the sixth segment (*Leptocerus*, *Odontocerum*, *Molanna*, *Mystacides*, etc.) or may terminate on the seventh segment (some species of *Limnophilus*, *Lepidostoma*, *Goëra*, etc.). In *Plectrocnemia* it terminates on the eighth segment. *Odontocerum albicorne* (fig. 9, F) is unique in possessing sac-like organs attached to the anterior plates. The posterior plate of the fifth segment only is provided with hooks. These are two in number. In *Hydroptila occulta* there is a single pair of anterior plates on the third segment, two pairs on the fourth, fifth and sixth, and one pair on the seventh. The posterior plate on the fifth segment is absent.

Anal processes.—Considerable variation in shape of the posterior end of the abdomen is found in the different families. In the pupae from campodeiform types of larvae (Rhyacophilidae, Philopotamidae, Hydroptilidae, Polycentropidae, Psychomyidae) the pupal integument more nearly follows the shape of the underlying adult genitalia, although in Hydropsychidae there is a pair of two-segmented blunt appendages. In the Phryganeidae the pupal integument is a simple envelope to the genitalia. On the other hand, in all the other families there is an elaboration, to a greater or lesser degree, of the last abdominal segment to form a pair of acicular processes. These are single-pointed and devoid of bristles in *Odontocerum albicorne* (the sole British species of the Odontoceridae) and Goërinae. Emphasizing the diverse assemblage in the Sericostomatidae the anal processes in the Lepidostomatinae are short, triangular, confluent at their bases and very hairy—in contrast to the Goërinae. In the Limnophilidae, Molannidae and Leptoceridae they are long and slender, but usually blunt at the tip, with a few short bristles and sometimes some small hooks. A diversity of form is found in the Beraeidae, whilst in the genus *Beraeodes* the anal processes are long and slender with a few long hairs. In *Beraea* they are short, broad at the base and furnished with a large number of shorter hairs.

The function of these processes is generally thought to be the cleansing of the orifices in the plug of the cocoon—similar, in fact, to the large bristles on the front of the head. The movement of the abdomen during the current-forming rhythmic undulations would cause the anal processes to clear silt, etc., from the orifices. This function fits in well with the facts. Thus the processes are absent in those cases where well-defined terminal orifices are not present.

Gills.—In those families with campodeiform larvae, gills are usually absent in the pupa even though gills may be present in the larvae (e.g. *Rhyacophila*). In the Polycentropidae, however, abdominal filiform gills are present although absent in the larva, and in the Hydropsychidae tufted gills are present in the pupa similar to those of the larva, but generally not so numerous. In all the families with eruciform and sub-eruciform larvae, gills are present in the pupa if they are present in the larva (which is more usually the case), but almost always some slight reduction in numbers or disposition occurs.

Key to the families of Trichoptera based on the pupal skin.

1. Mandibles with several large teeth . . . . 2.
   Mandibles with no teeth, small or minute teeth only . . . . . . 4.
2. Mandibles very hairy at the base, anal processes long, very hairy, sclerotized apices . . . . Hydropsychidae.
   Mandibles with two bristles only at the base, anal processes short, not hairy and without sclerotized apices. . . . . 3.
3. Mandibles sharply bent near the base, symmetrical . . Philopotamidae.
   Mandibles not bent, asymmetrical . . . . Rhyacophilidae.
4. Mandibles with two bristles emerging from conical projection on outer edge of base . . . Phryganeidae except *Neuronia clathrata*.
   Mandibles without conical projection on outer edge of base from which bristles emerge. . . . . 5.
5. Anal processes absent or very short and broad at the base . . . 6.
   Anal processes long and slender . . . . 9.
6[1]. Small auxiliary dorsal hook-bearing plates on abdominal segments 3, 4 and 5 (see fig. 9, k). Pupae very small . . . Hydroptilidae.
   Auxiliary dorsal hook-bearing plates not on abdominal segments 3, 4 and 5. Pupae medium size . . . . 7.
7. Mandibles with long, thin apical part curved with a few teeth at the apex or strongly curved at the junction of the thin part with the base, and curved again near the apex without teeth Psychomyidae.
   Mandibles without long thin apical part . . . . 8.
8. Hook-bearing plates on 1st abdominal segment bracket-shaped and joined by a transverse sclerotized bar. Hook-bearing plates on segments 3, 4, 5 ant. and 5 post., 6 and 7 Sericostomatidae (Lepidostomatinae).
   Hook-bearing plates absent on 1st and 7th abdominal segments Polycentropidae.

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[1] From this point onwards the key should be used with some reserve, as only representative species in the families have been examined.

9. Dorsal hook-bearing plates sac-like except that on the posterior 5th segment which has two hooks. Hook-bearing plate on 6th segment continuous with a sclerotized bar.
   ODONTOCERIDAE. *Odontocerum albicorne* Scopoli. Sole British species.
   Dorsal hook-bearing plates not sac-like—that on the 6th segment not continuous with a sclerotized bar . . . . 10.
10. Antennae long, curved around posterior abdominal segments with forwardly directed lappets on 9th segment . . . LEPTOCERIDAE.
   Antennae not curved around posterior abdominal segments, lappets on 9th abdominal segment absent 11
11. Posterior margin of 1st abdominal segment with two bulbous projections beset with spicules or with two well-defined spicule-bearing patches . . . . 12.
   Posterior margin of 1st abdominal segment without spicule-bearing projections or patches . . . . 13.
12. Pair of bulbous projections with spicules on posterior margin of 1st abdominal segment . . . . LIMNOPHILIDAE.
   Bulbous projections on posterior margin of 1st abdominal segment absent
   SERICOSTOMATIDAE (GOËRINAE, BRACHYCENTRINAE, SERICOSTOMATINAE.)
13. Lateral line present . . . . MOLANNIDAE.
   Lateral line absent . . . . BERAEIDAE.

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CONTENTS

PAGE

Tottenham, The Rev. C. E., M.A., F.R.E.S.
Studies in the genus *Philonthus* Stephens (Coleoptera) . . . . 291–362, 175 figs.

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STUDIES IN THE GENUS *PHILONTHUS* STEPHENS (COLEOPTERA).

By the Rev. C. E. Tottenham, M.A., F.R.E.S.

(*Department of Zoology, University of Cambridge.*)

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(Read 5th October, 1949.)

With 175 Text-figures.

The purpose of this paper is twofold: firstly to figure the aedeagus of as many African species of the genus *Philonthus* Stephens as possible, and secondly, to describe a number of new species belonging to that genus.

I. Some African Species.

Up to the present date the known species of *Philonthus* which have been described from Africa, or recorded from that continent (exclusive of the Mediterranean area), number nearly two hundred. The majority of them fall into the former category. Some species, well known in other parts of the world and reputed to occur in Africa, require further confirmation. The determination of African material of the genus is beset with difficulties. Existing descriptions are scattered over numerous publications, comparatively few ever occurring together in the same work; many of these works are costly and difficult of access. Having obtained the descriptions of every species of the genus (not only from Africa, but from the whole world), I found another great difficulty in the inadequacy of many of them. Some of them are too brief; in some no comparison is made with other species; in some a new species is likened to another species which is very dissimilar to it; and the most reliable character for the determination of the species was entirely omitted from all[1]. Another difficulty which had to be faced was the comparative lack of material with which to work. Not only was the number of accessible species small, but the species were represented by very short series, often only one or two specimens.

With these difficulties to contend with, there is always the possibility of describing as new an already described species. Every possible care has been taken not to do so. The risk, however, of an extra name or two, which may have to be sunk subsequently as a synonym, is preferable to the confusion which is likely to follow in the wake of wrongly determined specimens.

An examination of the types of all the African species was, of course, out of the question. Although a number of types have been seen, it has been necessary to assume as correct those determinations which have been made by

[1] Since this was written descriptions of a few African species by French authors have been published (or become accessible in Great Britain) to which this remark does not apply.

others, provided that they tallied with the descriptions. By figuring the aedeagus I believe I have been able to give a precise indication of the species referred to under each name, and thereby eliminate future confusion or errors resulting from mistaken identifications, if there are any, in this paper.

Sources of Material used.

(1) *The British Museum* (*Natural History*).—Through the kindness of the authorities in the Museum, I have been enabled to examine the aedeagus of many species. Many of the new species described in this paper are represented in the collection of the British Museum. Nearly all of these have been in the collection, to my knowledge, for about fifteen years, standing over names which have never been published. The labels over which they stood in the cabinet drawers, and often also tickets on the specimens themselves, attribute the trivial names to Bernhauer. Shortly before the war I wrote to him with regard to these species, in case I had overlooked their descriptions; in doing so I mentioned a number of them by name. He replied that they were not his and that, although they were well-known species, no published descriptions existed. In view of the fact that most of these species have been so long with unpublished names, that Bernhauer has stated that many of them are not his, and finally that that author is now dead, I feel that it is time that something were done in the matter and that the beetles in question should be described. I do so in this paper, using whenever possible the names on these Museum labels. Where a change has been necessary, owing to the fact that the manuscript name is a homonym, the fact has been stated in the text, together with a reference to the MS. name which the new name supplants.

A few species in the collection I have deliberately omitted from this paper, either because I am not satisfied that they represent new species, or because the available material was insufficient to enable a sound opinion to be formed as to their status, or because the specimens were females and belonged to groups in which the aedeagus is essential for identification.

(2) *Musée du Congo Belge.*—I am deeply indebted to Dr. Schouteden for his kindness in sending me some material of the genus both for determination and for study. I was thus enabled to examine the genitalia of a number of species not represented in the British Museum, and also to study some types.

(3) *My own collection.*—Although poor in African material, it has provided a few more species to be added to the number of those studied.

The aedeagus.

The aedeagus in the genus *Philonthus* normally consists of two lobes, the median lobe (" penis " of some authors) and the paramere, which lie adjacent to one another, united to each other at the base of the paramere. The basal portion of the median lobe, i.e. the part before the junction of the paramere, is bulbous, and since this part is liable to a certain amount of shrinkage or distortion in dried specimens, no importance must be attached to its exact shape in the figures. The characters of value for the determination of the species lie in the outline of the median lobe viewed dorsally or laterally, the outline of the paramere, the relative lengths and widths of the two, and the arrangement of the "pegs" on the inner face of the paramere. The internal sac is invaginated apically from the outer face of the median lobe; since, therefore, this region of the median lobe is softer than the rest of the organ, and since the internal sac is often partially or wholly evaginated and hardened in dried specimens, the exact outline of the lobe, when viewed laterally, is not always easy to detect. At, or near the apex, the paramere bears some hairs; these, too, are often very difficult to detect, and in dried specimens apt to be missing; except, therefore, where these hairs were obvious, I have refrained from putting them in the figures.

It would be impossible to over-emphasize the importance of the aedeagus as a character for the identification of the species of the genus *Philonthus*. In this genus, as in many others, in the majority of cases the structure of the aedeagus is very constant within a species, and furthermore, the differences presented by this organ between the species are often very marked. It is a curious fact that very often there is little difference in the aedeagal characters of two species which in other respects can be easily determined, but the differences are great between species otherwise hard to distinguish. In fact, as a general rule, within the genus *Philonthus*, it can be said that the aedeagus affords both the most reliable and the easiest character for the determination of the species. I believe it would be true to say (1) that very nearly all the African species of the genus could be identified by means of the aedeagus alone without any reference to descriptions, and (2) that identifications based upon the aedeagus would have a far greater reliability than those based on descriptions and/or comparison with named specimens. It is certainly true to say that some species of *Philonthus* (even if *Gabrius* be regarded as a distinct genus) cannot be determined without resort to the aedeagus.

It is because of the importance of this character that I have deliberately refrained from describing some new species, based upon female specimens only, in groups where it is known that the aedeagus is important. In a few cases, in groups where, so far as is known at present, species can be separated without recourse to the aedeagus, I have described a few new species based upon females; in this I was prompted by the fact that some of them were already in Museums standing over the unpublished names. It is, however, a doubtful question whether it is justifiable to describe any species of the genus without figuring the aedeagus. When all is said and done, the primary purpose of a description of a species is not just to validate a name, but to make it possible for other workers to recognize the species. It is an extraordinary thing, therefore, that the most valuable character, the aedeagus, should have been neglected. Faunistic and other studies depend largely for their value on the accuracy with which the species are determined and it is a pity that only too often the systematic work on which they depend is not sufficiently up-to-date and reliable.

With a view to contributing a greater precision to determinations the aedeagus has been studied and figured in this paper. A mere glance at the figures will be sufficient to show the great range of variety which the organ presents within the genus, and to carry conviction as to the utility of the aedeagus as a means of identification for the species.

It would be premature at this stage, considering that barely half the known African species have been studied, to form any theories as to the evolution of the various forms exhibited in these species. On the other hand, it is justifiable to call attention to a few facts. Firstly, in contrast to the comparative conformity to a few standardized types exhibited by the European or North American species, the African species exhibit a much greater range of form. Two quite exceptional forms must be noted, namely, the paramere of *P. schoutedeni* Bernhauer, which bears two extra lobes which carry the pegs and some of the hairs, and *P. biparamerosus* sp. n., which possesses two parameres. Again there are some noticeable instances of asymmetry, such as *P. sanguineus* Fauvel, and the species of the *longicornis* group; the latter species, so well-known in Europe, being apparently cosmopolitan. In *P. densecaudatus* Bernhauer there is a distinct shoulder near the base of the paramere, suggestive of a rudimentary second paramere or of a lost branch of a forked paramere. The *longicornis* group are of special interest in Africa for they may possibly prove to be a case in which the aedeagus fails to be of any value as a specific character in some of the species, if they are, in fact, species and not merely varieties or local races.

I have omitted from the figures those species, such as *P. longicornis* Stephens, *P. quisquiliarius* Gyllenhal, etc., which form part of the European fauna; these I hope to deal with in a future paper.

The Head.

Except for colour in relatively few species and except for size, probably due to food supply in the larval state, the species of *Philonthus* display but little variation in their characters. An exception, however, must be made of the head, which in a number of species is subject to great variation, especially in the males. Speaking very generally this variation occurs mostly in the species with more quadrate transverse heads than in the more elongate, round-headed species. It is especially noticeable in the species of the *politus* L. group. A series of measurements of heads of male *politus* showed that the largest head measured was 1·8 times the smallest in actual width; and that the proportions of width : length ranged from 1·54 to 1·09. It follows that in an exact description of a unique male, the description so far as the head is concerned, must be regarded as the description of the head of a specimen rather than that of the head of the species.

Terminology.

(a) *The abdomen.*—In descriptions of species of the genus considerable discrepancy may be found in the number by which any particular abdominal segment is designated. The discrepancies may sometimes be due to error, sometimes to differences of notation, since not all the tergites are visible. Again, more tergites exist than sternites, therefore if these are counted irrespective of the segment to which they belong, a different number has to be employed for the tergite of a segment from that employed for its sternite. Recent authors have often overcome the difficulty of ambiguity with regard to the tergites by making their meaning clear in the text, e.g. " das dritte und vierte (erste und zweite freiliegende) Tergit" or " fifth tergite (third visible) "; this has the great advantage of clarity and accuracy, but is rather cumbrous. In the descriptions which follow I have adopted the method of using the number of the segment for the tergite and sternite of that segment; thus " eighth tergite " means the tergite of the eighth segment, " eighth sternite " means the sternite of that segment. The eighth segment is the segment before the last, i.e. before the segment bearing the long paraprocts. It is the eighth segment which in *Philonthus* has the sternite emarginate in the male.

(b) *The thorax.*—Most of the species of *Philonthus*, as is well known, have two longitudinal series of punctures on the disc of the thorax. These punctures differ in number according to the species, and form convenient groups into which to divide the genus. The anterior puncture of each series is situated very close to the anterior margin of the thorax. Some authors have followed the Erichson notation of including the anterior puncture in the discal series, while others, such as Fauvel and Eppelsheim, have regarded it as being one of the marginal punctures. Thus the 4-punctate group of Fauvel is the 5-punctate group of Erichson. I have followed the Erichson notation in this paper, as has been done by the majority of authors, including Bernhauer and Cameron.

(c) *The aedeagus.*—Since the aedeagus lies in the abdomen in a different position from that which it assumes when extruded, ambiguities can arise as to the meaning of "dorsal" and "lateral" view. Although the description of the aedeagus and figures will generally serve to make it clear what the author means by these terms, yet, strange as it may seem considering the structure of the aedeagus, there are cases in which it is not possible to tell whether by "dorsal" he meant "dorsal" or "ventral," although it was clear what he meant by "lateral." In the genus *Gabrius* the aedeagus lies in the abdomen in a different position from that in which it lies in *Philonthus*. For purposes of description, therefore, I have considered it simplest to treat the aedeagus by itself, irrespective of the position it occupies in the abdomen or when extruded. If the aedeagus be mounted with the paramere lying uppermost, the view thus obtained I call the "upper view" or "viewed from above"; if the aedeagus is placed with the paramere lying alongside the median lobe, we get the "lateral view" of this paper. The inner surfaces of the paramere and median lobe are the surfaces of these two parts which face one another. Figure 1, for example, is upper view, and shows the outer surface of paramere and the inner surface of median lobe. Figure 4 is a lateral view. In a number of cases I have only figured the apical portion of the aedeagus, or of the median lobe or paramere, as it is here that the important distinctions lie.

In some cases, where the position could be detected without removing the paramere, and sometimes to economize in space, I have indicated the pegs on the paramere as shown in the upper view; it must be clearly understood, however, that the pegs are really on the inner face.

For purposes of identification, the species of the genus can be divided into groups as follows:

Group 1. No discal series of punctures on thorax . . . . p. 296
,, 2. Discal series of thoracic punctures consisting of 1, 2 or 3 punctures each . . . . p. 299
,, 3. Discal series of thorax consisting of 4 punctures each . . . p. 304
Section A.—Large black species or species related to *P. politus* L. p. 305
Section B.—Small or moderate-sized species . . . . . p. 317
,, 4. Discal series of thorax consisting of 5 punctures each . . . p. 328
,, 5. Discal series of thorax consisting of 6 punctures each . . . p. 345

Group 6. Discal series of thorax each consisting of more than 6 punctures, series often very irregular . . . . p. 356

,, 7. Large brown species, discal series of thorax consisting of various numbers of punctures . . . . p. 359

Group 1.—*Discal Series of Thoracic Punctures Absent.*

In this group are two African species, *impuncticollis* Bernhauer and *curiosus* sp. n. In other parts of the world the group is represented by very few species, and it appears to be a group of convenience for the purpose of separating off some of the species of this large genus, rather than a natural group of allied species. *P. impuncticollis* Bernhauer bears a general resemblance to species of the *politus* group, and perhaps should be more naturally classed with these; *P. curiosus* sp. n., on the other hand, is of a Quedioid appearance and unlike any other species of the genus known to me.

These two species may be separated thus:

1. Size larger, 14 mm.; facies of *politus* Linnaeus; median pair of interocular punctures present; elytra bronze, as long as broad
1. *impuncticollis* Bernhauer.[1]

Size smaller, 11 mm.; facies of *Quedius*; median pair of interocular punctures absent; elytra pitchy-brown, much broader than long
2. **curiosus** sp. n.

1. *P. impuncticollis* Bernhauer.

Bernhauer, 1932, *Rev. Zool.-Bot. afr.* 22 : 153.

Since Bernhauer's description of this species is very short and consists merely of the differences between it and *splendens* Fabricius, I give here a full description of the species taken from an unnamed specimen in the Belgian Congo Museum which seems to be the Bernhauer species and which comes from the type locality, namely, Haut-Uele, Abimva. The figure of the aedeagus is taken from this specimen.

In size and general appearance very like *P. politus* L., from which it may be distinguished easily by the absence of the discal series of punctures on the thorax, by the less punctate head, by the absence of "brackets" at the bases of the abdominal segments, etc. The aedeagus is very like that of *P. addendus* Sharp.

Black; elytra bronze; legs, antennae and palpi pitchy-brown.

Head (male) transverse, about one-quarter broader than long; front almost straight, slightly convex, anterior angles very obtuse; eyes large, extending two-thirds of the side of the head; surface smooth, shining, with five or six punctures along the inner margin of the eye; the median pair of interocular punctures very widely distant from one another, situated quite close to the front marginal punctures of the eyes; two other punctures between the latter and the base of the antenna; a cluster of punctures in the post-ocular region; sides of head slightly divergent towards the base; posterior angles obtusely rounded; basal margin rounded, concave.

Mandibles short and stout, the right mandible longer, sharper and more slender than the left; the inner margin very strongly and bluntly toothed in the middle.

Maxillary palpi with the last segment long, narrow, but little pointed at the apex, much longer than the third, which is shorter than the second.

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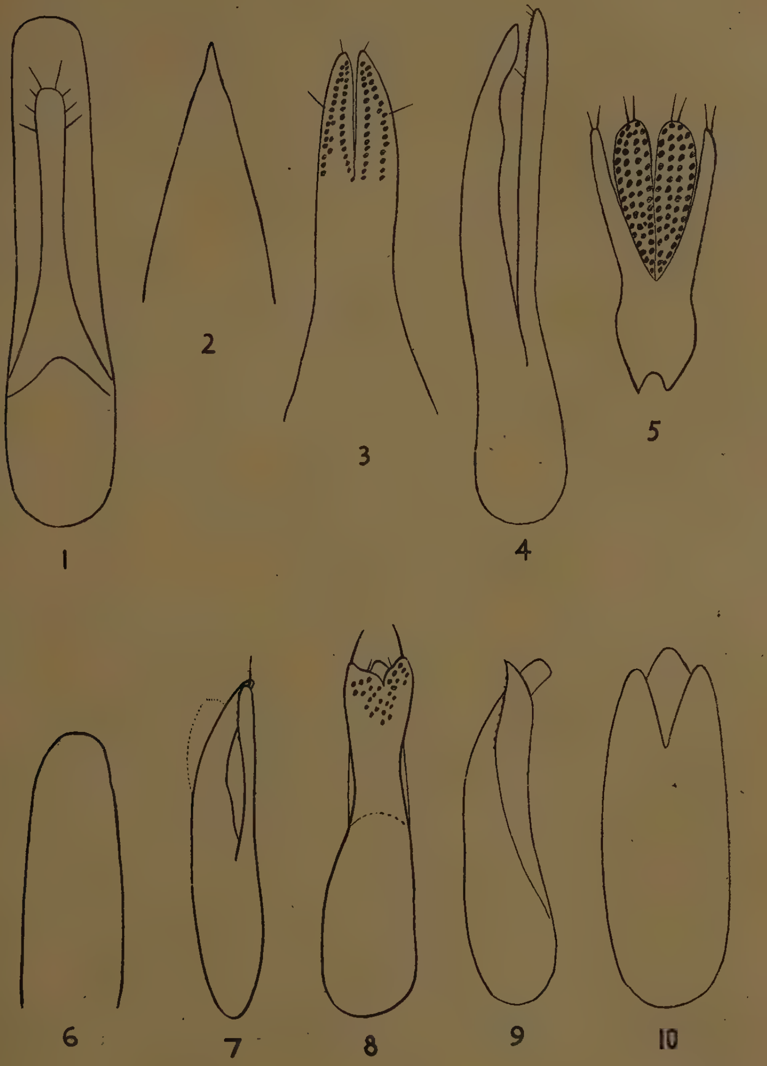
[1] Numbers placed in front of the names of species in the keys indicate that these species are referred to in the text of this paper.



FIGS. 1–10.—(1) *P. impuncticollis* Bernhauer. Aedeagus, upper view. (2) *P. curiosus* sp. n. Apex of median lobe, inner face. (3) *P. curiosus.* Apex of paramere, inner face. (4) *P. curiosus.* Aedeagus, lateral view. (5) *P. schoutedeni* Bernhauer. Paramere, inner face. (6) *P. schoutedeni.* Apex of median lobe, inner face. (7) *P. seriatipennis* Bernhauer. Aedeagus, lateral view. (8) *P. seriatipennis.* Aedeagus, upper view. (9) *P. triseriatus* Bernhauer. Aedeagus, lateral view. (10) *P. triseriatus.* Aedeagus, upper view.

Antennae gradually, but not much, thickened towards the apex; second and third segments equal, considerably shorter than the first; fourth a little longer than broad; fifth quadrate; sixth to tenth increasingly transverse; eleventh short, as long as broad at its shortest length.

Thorax in front about as broad as head, widened behind; viewed from above, the anterior angles are deflexed and broadly rounded, viewed from the sides they are nearly right angles; sides slightly rounded; the posterior angles and the base form one broad continuous curve; discal series of punctures absent; usual marginal punctures and four punctures in the anterior angles.

Scutellum moderately closely punctured.

Elytra about as long as together broad; bronze-olive in colour, clothed with dense, long, yellowish pubescence; puncturation close and moderately strong, nearly as close as that of *P. politus* L.

Abdomen finely and fairly thickly punctured, but not so closely as in *politus* L.; the transverse lines at the bases of the segments are straight.

Posterior tarsi with the first segment short, about equal in length to the fifth, shorter than the three following together. Legs short, densely pubescent, with the tibiae strongly spinose.

Male: Anterior tarsi distinctly but not very broadly dilated. 8th sternite very broadly, shallowly, triangularly excised at the apex.

Length: 14 mm.

Aedeagus with the median lobe rather broad, parallel-sided, and flatly rounded at the apex; paramere slender, about one-third the width of the median lobe, a little widened towards the apex, where it is rounded (fig. 1).

2. **P. curiosus** sp. n.

In the British Museum there is a short series of this species standing over the MS. name "*paradoxus* Bernhauer." I have rejected this name, since it has already been employed for an Indian species of the genus by Cameron (1932, *Fn. Brit. Ind. Staph.* **3**: 151).

Head black; thorax pitchy black; elytra pitchy brown; abdomen pitchy black, the segments with the side margins and the apical margins brown; palpi pitchy; antennae brown, with the apex of each segment infuscate; legs dirty testaceous.

Head a little broader than long, widest behind eyes; sides behind eyes rounded and narrowed; eyes large, occupying three-quarters of the sides of the head; base straight, neck wide; a minute puncture at the inner margin of the eye anteriorly; no interocular punctures; a few distinct punctures in the post-ocular region; surface with a distinct, more or less transverse ground sculpture.

Maxillary palpi with the last segment longer than the penultimate.

Antennae very short, shorter than the head and thorax together; third segment shorter than the second; fourth and fifth subequal; sixth to tenth transverse; eleventh short, equal to the fourth.

Thorax distinctly longer than broad; sides slightly rounded, convergent anteriorly, more or less parallel posteriorly; anterior angles deflexed, marked; posterior angles obtuse, rounded together with the base.

Scutellum a little more finely and more closely punctured than the elytra.

Elytra longer than the thorax; much broader than long; finely, moderately closely punctured; pubescence long, yellowish.

Abdomen diffusely and finely punctured, shining; pubescence scanty.

Legs short; posterior tarsi longer than the tibiae; first segment equal to fifth, as long as the second and third together.

Length: 11 mm.

Male : Anterior tarsi moderately dilated. I have not examined the structure of the last ventral segments. The aedeagus is rather curious, the median lobe being unusually broad basally and evenly narrowed to a point at the apex, the paramere being narrowly and deeply divided at the apex, studded with a double row of numerous pegs on the inner face at each side of the division (figs. 2, 3, 4).

N.W. RHODESIA ; Kashitu, N. of Broken Hill, 23.iii.1915 (*H. C. Dollman*). Type in the British Museum (Natural History)

The species has rather a Quedioid appearance, and is remarkable for the scarcity of punctures on the head and thorax. On the thorax the discal series is wanting (or only marked by one small puncture in the fourth position) ; there is no lateral series, only a few very minute punctures ; there are two distinct punctures near the margin and a very few minute marginal punctures.

Group 2.—*Discal Series of Thoracic Punctures Consisting of* 1, 2 *or* 3 *Punctures.*

As was the case in the previous group, the species in the present group, whether from Africa or from other parts of the world, are not numerous, neither do they, taken all together, form a natural group. It is significant, however, that a number of these species from the Congo region share in common a distinctive feature in the sculpture of the elytra, which consists of a few longitudinal series of larger setiferous punctures in addition to the normal punctuation. I have only been able to examine the aedeagus of three of these Congo species, and in each case the structure of this organ is exceptional. But whereas two of them, *triseriatus* Bernhauer and *seriatipennis* Bernhauer, differ from the normal form in a similar manner, the third, *schoutedeni* Bernhauer, differs from the normal in another way, so remarkable that I consider the species should be placed in a separate subgenus. An examination of the aedeagus of the other species of the group would be interesting.

Within the group also there are another three species which stand by themselves, namely, *madianus* Bernhauer, *rugulipennis* sp. n. and *peripateticus* sp. n. ; and these also, I consider, should be placed in a separate subgenus.

The following key to the species of the group has been drawn up largely from the published descriptions, and for reasons stated below (p. 304) *madianus* Bernhauer has been omitted from the key.

1. Elytra with a few longitudinal rows of larger punctures in addition to the other puncturation . . . . 2.
Elytra closely, rugosely, uniformly punctured . . . . 8.
2. Thorax with discal series consisting of one distinct puncture (the marginal puncture indistinct if also present) . . . . 3.
Thorax with discal series consisting of three punctures . . . . . 4.
3. Thoracic puncture situated behind the middle ; elytra closely, rather finely punctured . . . . *reinecki* Schubert.
Thoracic puncture before the middle ; elytra smooth, almost impunctate 3. *schoutedeni* Bernhauer.
4. Elytra unicolorous black . . . . 5.
Elytra not unicolorous black . . . . 6.
5. Basal segment of antennae and legs light ; abdomen almost impunctate along the middle ; size smaller, 5–6 mm. . . . . . *tristichus* Cameron.
Antennae and legs pitchy ; abdomen punctate ; size larger, 7·5–8·5 mm. *mongendensis* Bernhauer.

6. Elytra with extreme hind margins narrowly reddish . . . 5. *triseriatus* Bernhauer.
Elytra unicolorous brownish . . . . 7.
7. Size smaller, 5·5–6 mm.; elytra more finely and closely punctured, margins of abdominal segments lighter . . . 4. *seriatipennis* Bernhauer.
Size larger, 7·5 mm.; elytra less closely punctured; abdomen unicolorous black . . . . { *dilutior* Bernhauer. / *lampropterus* Bernhauer. }
8. Head transverse, quadrate, sides behind eyes straight, divergent, posterior angles marked, nearly rectangular. . . . 6. **rugulipennis** sp. n.
Head transverse oval, sides behind eyes feebly rounded, nearly parallel, posterior angles obtuse, rounded . . . . . . 7. **peripateticus** sp. n.

3. *P. schoutedeni* Bernhauer.

Bernhauer, 1928, *Wien ent. Ztg.* **45** : 115.

This species is remarkable because of the smooth surface of the elytra, which are almost devoid of puncturation; in this respect it is unique among all the species of the genus known to me. Furthermore, it is unique in the structure of the aedeagus. The paramere is widely furcate (as in many other species of the genus), but within the furcation it carries two large accessory lobes which bear the pegs which normally occur on the inner face of the paramere at the apex. These lobes are closely and entirely studded with the pegs. The hairs which are usually present at the apex of the paramere are situated partly at the apex of each prong and partly on these additional lobes. Figure 5 shows the paramere with accessory lobes; figure 6 is the apical part of the median lobe. The figures are drawn from a specimen in the Musée du Congo Belge from Haut-Uele : Dika.

This extraordinary aedeagus marks *P. schoutedeni* Bernhauer as being an exceptional form within the genus; and it is not without interest that it is accompanied by an extreme form of elytral sculpture. I consider that the aedeagal structure alone warrants placing the species in a separate subgenus, for which I propose the name **Philonthoblerius** subgen. n., with *Philonthus schoutedeni* Bernhauer as type.

4. *P. seriatipennis* Bernhauer.

Bernhauer, 1928, *Wien. ent. Ztg.* **45** : 114.
Cameron, 1929, *Rev. Zool.-Bot. afr.* **18** : 62.

In this species the aedeagus exhibits certain unusual features. The paramere at the apex envelops the median lobe on either side; it is also rather asymmetrical at the apex, where it is bilobed. The pegs are irregular and extend a considerable distance below the point of union of the two lobes (figs. 7 and 8).

5. *P. triseriatus* Bernhauer.

Bernhauer, 1928, *Wien ent. Ztg.* **45** : 112.
Cameron, 1929, *Rev. Zool.-Bot. afr.* **18** : 61.

In this species the aedeagus is similar to that of the previous species in the way that the apex of the paramere enwraps the median lobe at the sides, and also in the fact that the paramere is divided at the apex. It differs, however, in the shape of the paramere, and in the arrangement of the pegs which are not visible from the outer face.

I have seen three specimens of this species in the Musée du Congo Belge, each bearing the label "Type." From one of these specimens, from Mongende, I have figured the aedeagus (figs. 9 and 10).

6. **P. rugulipennis** sp. n. ✓

Black, with the palpi, base of the antennae, and legs brown, and with the apex of the apical segments of the abdomen brownish.

Head (male) distinctly transverse, rectangular, about one-third wider than long; front broadly rounded between the antennal tubercles, from these points to the eyes distinctly concave; sides behind eyes about equal to the length of the eye, slightly divergent posteriorly; posterior angles obtusely rounded; hind margin straight. There is a distinct longitudinal, oval impression on the vertex of the head between the antennae. Three punctures along the inner margin of the eye, one at the extreme front, two at the posterior angle; a fourth puncture near the eye forms a triangle with the two latter; median interocular punctures situated slightly posterior to the anterior marginal puncture of the eye, widely separated, being twice as distant from one another as from the eye; a group of numerous punctures in the post-ocular region.

Mandibles fairly long, strongly and bluntly toothed in the middle of the inner edge, apical part slender.

Maxillary palpi with the apical segment about equal to the penultimate.

Antennae not thickened, segments of equal width; second and third equal, about one-quarter the length of the first; fourth and fifth slightly longer than broad; fifth to tenth decreasing in length, the penultimate segments distinctly transverse; eleventh a little longer than broad.

Thorax as wide as the head (male), quadrate; anterior angles almost right angles; sides parallel; posterior angles broadly rounded together with the base. The two discal series consist of three punctures each, one on the anterior margin, one at about one-quarter the length of the thorax, and one at three-quarters the length. There are three other punctures between the second of these and the sides, in addition to usual marginal punctures. If viewed sideways the margin of the thorax will be seen to be strongly concave towards the posterior angle.

Scutellum equilateral; strongly and closely punctured.

Elytra broader than long; very closely, evenly and deeply punctured with large punctures.

Segments of the abdomen as closely punctured as the elytra, but the punctures are a little smaller and become much finer towards the apex.

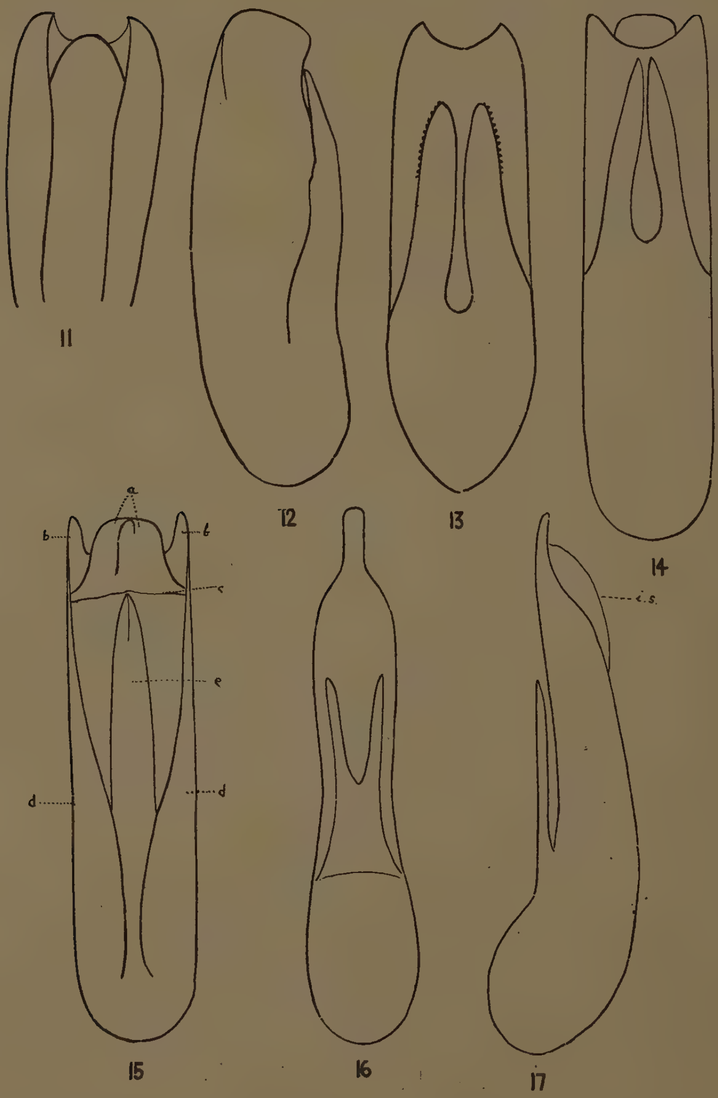
Legs with the tibiae strongly spinose and pubescent. Posterior tarsi with the first segment longer than the fifth, nearly as long as the three following together.

Underside with the head smooth, shining, with a few scattered punctures; abdomen closely, roughly punctured; anterior coxae lighter than the others.

Length: 12 mm.

Male: Anterior tarsi dilated; eighth sternite triangularly excised to a depth of about one-third the length of the segment. Aedeagus with the median lobe parallel-sided, semicircularly excavate at the apex; on the outer face the sides fold over to enclose a produced apical portion which is scarcely visible from the other side; the paramere is deeply, but not widely, divided, from the apex almost to the base, the division being a little wider towards the base; the pegs appear to be arranged along the outer margin of each of the two lobes thus formed, and are directed outwards, so that they are clearly visible when the aedeagus is viewed from the outer face of the paramere. (Figs. 11, 12 and 13.)

The above description has been drawn up from a specimen in the Musée du Congo Belge bearing the unpublished name, *rugulipennis*.



FIGS. 11–17.—(11) *P. rugulipennis* sp. n. Apex of median lobe, outer face. (12) *P. rugulipennis.* Aedeagus, lateral view. (13) *P. rugulipennis.* Aedeagus, upper view. (14) *P. peripateticus* sp. n. Aedeagus, upper view. (15) *P. peripateticus.* Aedeagus, lower view. (16) *P. bicolor* Fauvel. Aedeagus, upper view. (17) *P. bicolor.* Aedeagus, lateral view.

Holotype, in Musée du Congo Belge; Lulua: Kapanga, xi.1932 (*F. G. Overlaet*).

7. **P. peripateticus** sp. n.

Head and thorax black, shining; elytra and abdomen pitchy, dull; palpi reddish, light; legs and antennae pitchy brown, the latter with the basal segment lighter.

Head (male) broader than long (7·5 : 6·8), broadly rounded in front, rather straight between the antennae; sides behind eyes parallel; posterior angles large, obtusely rounded; base feebly concave; length of the eye equal to the distance from its hind margin to the bristle near the neck; median interocular punctures small and shallow, three times as distant from one another as from the marginal punctures of the eyes; three distinct punctures at the inner posterior angle of the eye; a number of other punctures in the post-ocular region; surface smooth.

Maxillary palpi with the apical segment subequal to the penultimate.

Mandibles short and stout.

Antennae short, gradually a little thickened towards the apex; third segment a little longer than the second; fourth a little longer than broad; fifth and sixth about as long as broad; seventh to tenth transverse; eleventh short.

Thorax slightly wider than the head (8·5 : 7·5), as long as broad; anterior angles rectangular, rounded; anterior margin truncate; sides nearly parallel, almost straight, feebly sinuate in front and behind; thorax broadest in the middle; posterior angles very obtusely rounded, together with the base. Discal series with two punctures in each, the first near the anterior margin being small; two punctures placed transversely on each side in line with the second discal puncture; another puncture in the anterior angle near the front margin.

Scutellum closely, moderately strongly and roughly punctured.

Elytra longer than the thorax (10 : 8·5), wider than long (10·5 : 10), wider at apex than at base (10·5 : 9·5); surface closely, strongly, coarsely punctured, with a very rough appearance; pubescence close, short, yellowish brown.

Abdomen very closely, evenly, rather finely punctured and pubescent throughout.

Legs with the tibiae pubescent and spinose; posterior tarsi as long as the tibiae; first segment nearly twice as long as the fifth, nearly as long as the three following together.

Length: 12 mm.

Male: Anterior tarsi rather strongly dilated; eighth sternite broadly emarginate at apex in a distinct, but not deep, curve, which is bordered by a smooth bevel.

In the aedeagus the paramere is divided for the greater part of its length; it is acuminate apically, where the two branches are approximate; towards the base of the division, however, they are quite widely separated; the paramere almost reaches the apical margin of the median lobe; there are two rows, each consisting of six or seven small pegs, arranged longitudinally at the apex on the inner face of each branch of the paramere. The median lobe is peculiar; in general form it is more or less tubular; viewed from the apical end it appears as a circle, with a gap on each side of the outer-face edge; viewed from the inner face (fig. 14) it is parallel-sided, with the apex strongly emarginate in a curve; behind the apical margin, exposed by this emargination, may be seen the apex of the outer face (?), which appears as a broad plate, flattened at its apex; viewed from the outer face the median lobe is very difficult to describe or to figure, and as I was only able to examine a dried specimen, it was impossible to tell to what extent the visible parts were internal sac. As may be seen from fig. 15, the back of the inner face may be seen apically at the sides (*b*); (*a*) is the broad plate referred to above; the inner face extends round the lobe more and more towards the base (*d*); the line (*c*) in the figure, so far as could be seen from the specimen examined, does not mark a separate part of the lobe, but indicates the beginning of a less sclerotized portion; similarly, (*e*) may not be a distinct plate, but is probably a more strongly sclerotized portion of the surface than the adjacent parts; there appears to be a distinct keel at the apex of this part (*e*).

Type in my collection, ♂; Nyassa; two paratypes from the same locality.

This species may be distinguished from the closely allied *rugulipennis* sp. n. by the rounded posterior angles of the head, absence of the depression on the vertex, and by the absence of the puncture in the fourth position of the discal series on the thorax; the puncturation of the abdomen is a little finer.

In view of the peculiar structure of the aedeagus in this and the preceding species, a peculiarity which is accompanied by similar differences in sculpture from the normal, I propose for these species a new subgenus, **Raucalius**, with *Philonthus peripateticus* sp. n. as its type.

8. *P. madianus* Bernhauer

Bernhauer, 1936, *Nov. Zool.* **39**: 263.

There is a specimen of this species, described from Angola, in the British Museum (Natural History). Bernhauer, in his description of the species, does not specify the type specimen but merely says, "In den Sammlungen des British Museums, des Museums in La Chaux-de-Fonds und, in meiner eigenen." Presumably the British Museum specimen may be regarded as a paratype at least. Unfortunately it is in a very bad condition, and I have been unable to separate it from *rugulipennis*. I have, however, felt justified in describing *rugulipennis* as a new species, since Bernhauer adopted this name for the species in question, although only as a museum label; and having examined other specimens of *madianus* it may be presumed that Bernhauer knew his own species and was able to detect differences between it and *rugulipennis* which are not readily discernible in a bad specimen. It is a pity that he did not figure or describe the aedeagus of *madianus*. Until such time as this organ can be examined I would provisionally place *madianus* Bernhauer along with *rugulipennis* and *peripateticus* in the new subgenus *Raucalius*.

Group 3.—*Discal Series of Thorax Consisting of Four Punctures.*

A large number of African species come in this group, and it is convenient for the purposes of a key to divide it.

First, all large or moderately large brown (or brown with black heads) species can be separated off and treated in a group by themselves, together with other similarly coloured species of other groups (Group 7). The number of punctures in the discal series of the thorax is not always easily discernible amongst these brown species, so it is an advantage to treat them by themselves instead of trying to place them in keys based on the thoracic punctures; no objection can be raised to this method of treatment on the grounds that such a grouping is a purely artificial one based on colour, for the grouping of species of *Philonthus* by their thoracic punctures is also an artificial one, and does not always show close relationship, but has always been found to be a practical method for the determination of species.

Secondly, some of the species in the four-punctate group are large, of the same general appearance and size as the well-known *P. politus* L.; these, together with a few other species of more or less the same size, I have placed in a key by themselves, Section A, leaving the small and moderate sized species to Section B.

Section A.

1. Abdomen brown . . . . . 9. *bicolor* Fauvel.
Abdomen black, or black with light apex . . . . . 2.
2. Abdomen with apex unicolorous with the rest . . . . . 3.
Abdomen black, with apex yellow ; elytra red-yellow 10. *flavicauda* Bernhauer.
3. Elytra red or crimson . . . . . 4.
Elytra otherwise coloured . . . . . 6.
4. Elytra red . . . . . 11. *affinis* Roth.
Elytra crimson . . . . . 5.
5. Head strongly transverse, wider behind, hind angles prominent ; elytra and abdomen rather diffusely punctured ; colour of elytra more crimson . . . . . 14. *haematodes* Bernhauer.
Head less transverse, not wider behind, hind angles obtusely rounded ; elytra and abdomen very closely and very finely punctured ; colour of elytra less crimson . . . . . 15. *scotti* Bernhauer.
6. Elytra blue . . . . . 12. *kristenseni* Bernhauer. & *chloropterus* Bernhauer.
Elytra not clear blue . . . . . 7.
7. Antennae with the first four or five segments testaceous 16. *dimidiaticornis* Fauvel.
Antennae with first four or five segments not all testaceous . . . 8
8. Elytra black with a red patch on the disc of each 23. *natalensis* var. *vittatus* Roth.
Elytra without red patch . . . . . 9.
9. Elytra metallic . . . . . 10.
Elytra unicolorous black, not metallic . . . . . 17.
10. Head quadrate, distinctly transverse . . . . . 11.
Head oval, or if quadrate as long as broad, ... 15.
11. Head and thorax black . . . . . 12.
Head and thorax metallic or coloured . . . . . 14.
12. Eyes occupying fully two-thirds the sides of the head ; elytra closely, fairly finely punctured ; scutellum densely and finely punctured all over . . . . . 17. *basicornis* Eppelsheim.
Eyes occupying less than half the sides of the head . . . . . 13.
13. Head with few punctures in the posterior angles ; elytra coppery, strongly but not closely punctured ; thorax more transverse 18. *carpenteri* Bernhauer.
Head with numerous rather strong punctures in the posterior angles ; elytra greenish-blue, strongly and closely punctured ; thorax less transverse . . . . . 19. **phoculus** sp. n.
14. Head and thorax greenish ; elytra green . . . . 20. *jeanneli* Bernhauer.
Head and thorax purple ; elytra greenish-bronze . . 21. **hirsutus** sp. n.
15. Head oval, transverse ; elytra bronze . . . . 13. *methneri* Bernhauer.
Head quadrate, about as long as broad 16
16. Eyes moderate, occupying about half the sides of the head ; elytra with steel-blue tint . . . . . *tandanlensis* Bernhauer.
Eyes very small, occupying scarcely one-third the sides of the head ; elytra bronze . . . . . 22. **abdicans** sp. n.
17. Puncturation of elytra very sparse ; insect narrow
24 *abyssinus* Fauvel.
25. *pseudabyssinus* Tottenham.
26. *elgonensis* Tottenham.
Puncturation of elytra moderately or very close . . . . . 18.

18. Segments four to six of antennae longer than broad . . . . 19.
 Segments four to six of antennae not longer than broad ; insect broad and convex ; elytra moderately punctured ; posterior angles of head not very strongly or closely punctured . 23. *natalensis* Boheman.
19. Size larger, species broader ; posterior angles of head with only a few strong punctures ; elytra rather strongly punctured 27. **nimboides** sp.n.
 Size smaller, insect narrower ; posterior angles of head with a few moderate punctures ; elytra closely and finely punctured 28. *aethiops* Bernhauer.

(*N.B.*—Nearly all the species belonging to the section are included in the above key.)

9. *P. bicolor* Fauvel

Fauvel, 1903, *Ark. Zool.* **1** : 240.

I have figured the aedeagus of this species from a specimen in my collection which I received without data, but bearing two labels, " *bicolor* Fauvel " and " *divisus* Sharp." The specimen is certainly not the latter species, with which I have compared it in the British Museum ; it answers to the description given by Fauvel of his species. The brown abdomen marks the species as quite distinct from the other known African species of the group. The aedeagus is not of the typical *politus* form, but has the paramere furcate ; the strongly narrowed and produced apex of the median lobe is also an unusual feature (figs. 16, 17).

10. *P. flavicauda* Bernhauer.

Bernhauer, 1936, *Ann. Mag. nat. Hist.* (10) **18** : 325.

This species is easily recognized by the pale apex to the abdomen. I have figured the aedeagus from a specimen in the Musée du Congo Belge from Kivu : Tshibinda. (Figs. 18, 19).

11. *P. affinis* Roth.

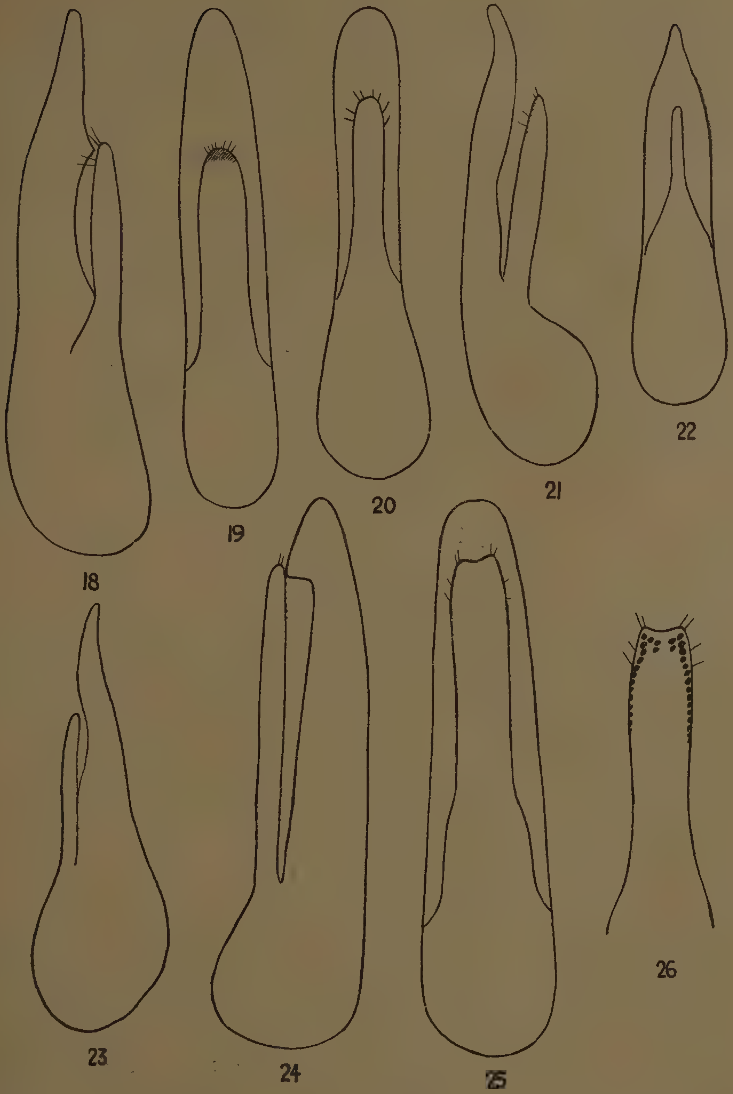
Roth, 1851, *Arch. Naturg.* **17** (1) : 118

The not easily accessible description of this species, which was described from Abyssinia, consists only of a few lines. I take this opportunity, therefore, of giving a full description of the insect and of figuring the male genitalia.

Head and thorax dark metallic green, elytra testaceous red, scutellum and abdomen black, antennae pitchy with base of second segment red, mandibles pitchy red, palpi reddish brown, tibiae and tarsi testaceous red, femora dark brown or blackish.

Head somewhat variable, transverse ; front feebly rounded ; sides slightly divergent posteriorly, nearly straight ; posterior angles rather obtuse and rounded ; eyes rather small, in length about equal to the sides behind the eyes ; interocular punctures more than twice as distant from one another as from the marginal puncture of the eye ; another strong pair of punctures as far apart as the interocular punctures, about the level of the hind margin of the eye, forming with the interocular punctures a rectangle ; vertex of head smooth, head finely punctured anteriorly, the whole of the postocular region filled with large punctures, this punctate area being more or less bounded by a line drawn from the posterior angle of the eye to the centre of the hind margin of the head.

Antennae with the second and third segments subequal, the fourth and fifth considerably shorter, but both a little longer than broad, sixth and seventh quadrate, eighth to tenth transverse.



FIGS. 18–26.—(18) *P. flavicauda* Bernhauer. Aedeagus, lateral view. (19) *P. flavicauda*. Aedeagus, upper view. (20) *P. affinis* Roth. Aedeagus, upper view. (21) *P. affinis*. Aedeagus, lateral view. (22) *P. haematodes* Bernhauer. Aedeagus, upper view. (23) *P. haematodes*. Aedeagus, lateral view. (24) *P. basicornis* Eppelsheim. Aedeagus, lateral view. (25) *P. basicornis*. Aedeagus, upper view. (26) *P. basicornis*. Apex of paramere, inner face.

Thorax as wide as the head and as long as wide; anterior margin truncate, anterior angles rectangular, sides nearly straight in front, but diverging posteriorly, so that the thorax is distinctly widest at about the middle, sides behind the middle sinuately narrowed to the posterior angles which are strongly rounded together with the base; dorsal series consisting of four fairly strong, more or less equidistant punctures; usual lateral punctures.

Scutellum rather finely and closely punctured.

Elytra quadrate, moderately closely and moderately strongly punctured and with yellowish pubescence.

Abdomen less closely and more finely punctured than the elytra, the lines at the bases of the segments straight.

Legs with the tibiae strongly spinose and pubescent; posterior tarsi with the first segment about equal to the fifth and scarcely as long as the second and third together.

Length: 16 mm.

Male: Anterior tarsi not strongly dilated; eighth sternite triangularly emarginate, the excision being a little wider than deep. The aedeagus, figs. 20, 21, calls for no special comment.

The species may easily be separated from the other species of the same size with 4-punctate thorax and red elytra (the European *P. nitidus* Fabricius, and the Central American *P. hogei* Sharp and *P. testaceipennis* Erichson) by its metallic green head and thorax, by its light legs, as well as by differences of sculpture.

12. *P. kristenseni* Bernhauer.

Bernhauer, 1915, *Ann. Mus. nat. Hung.* **13**: 138.

I have not seen any examples of this species and have included it in the key from the published description. There is evidently some confusion as to its identity, for I have seen specimens named by Bernhauer as this species which are *hospes* Erichson, a species belonging to the 5-punctate thorax group.

13. *P. methneri* Bernhauer.

Bernhauer, 1915, *Ann. Mus. nat. Hung.* **13**: 139.

There is a short series of *P. methneri* Bernhauer in the British Museum, but I have not been able to examine the aedeagus of a male.

14. *P. haematodes* Bernhauer.

Bernhauer, 1915, *Ann. Mus. nat. Hung.* **13**: 138.

The aedeagus is figured from a specimen which is identical with the *P. haematodes* Bernhauer in the British Museum. The specimen in question was among the Museum series of *methneri* Bernhauer and bears a Bernhauer label "*P. methneri*." The aedeagus is of the typical form and is shown in figs. 22, 23.

15. *P. scotti* Bernhauer.

Bernhauer, 1931, *J. Linn. Soc.* (*Zool.*) **38**: 586.

This species has been included in the key from the examination of a female specimen in the British Museum.

16. *P. dimidiaticornis* Fauvel.

Fauvel, 1905, *Rev. Ent.* 24 : 197.

This species is unknown to me, and I have relied on the published description to include it in the key. Fauvel's remark that it is of the facies of *P. proximus* Kraatz, and his other reference to that species are not affected by the confusion which has existed with regard to Kraatz's species. (*See* Tottenham, 1939, *Ent. mon. Mag.* **75** : 218–220.)

17. *P. basicornis* Eppelsheim.

Eppelsheim, 1895, *Dtsch. ent. Zeits.* 39 : 124.

This species is a very typical example of the group, and comes near to *P. politus* L. In the aedeagus, however, it shows a slight departure from the typical form. The paramere is rather broad and slightly emarginate at the apex, and the median lobe when viewed from its side has a distinct hook on the inner face at the apex, a character which occurs in some other species of the genus, and which is by no means uncommon in other genera of STAPHYLINIDAE. The form of the aedeagus is shown in figs. 24, 25, 26.

18. *P. carpenteri* Bernhauer.

Bernhauer, 1937, *Ann. Mag. nat. Hist.* (10) 20 : 301.

The aedeagus is shown in figs. 27, 28.

19. **P. phoculus** sp. n.

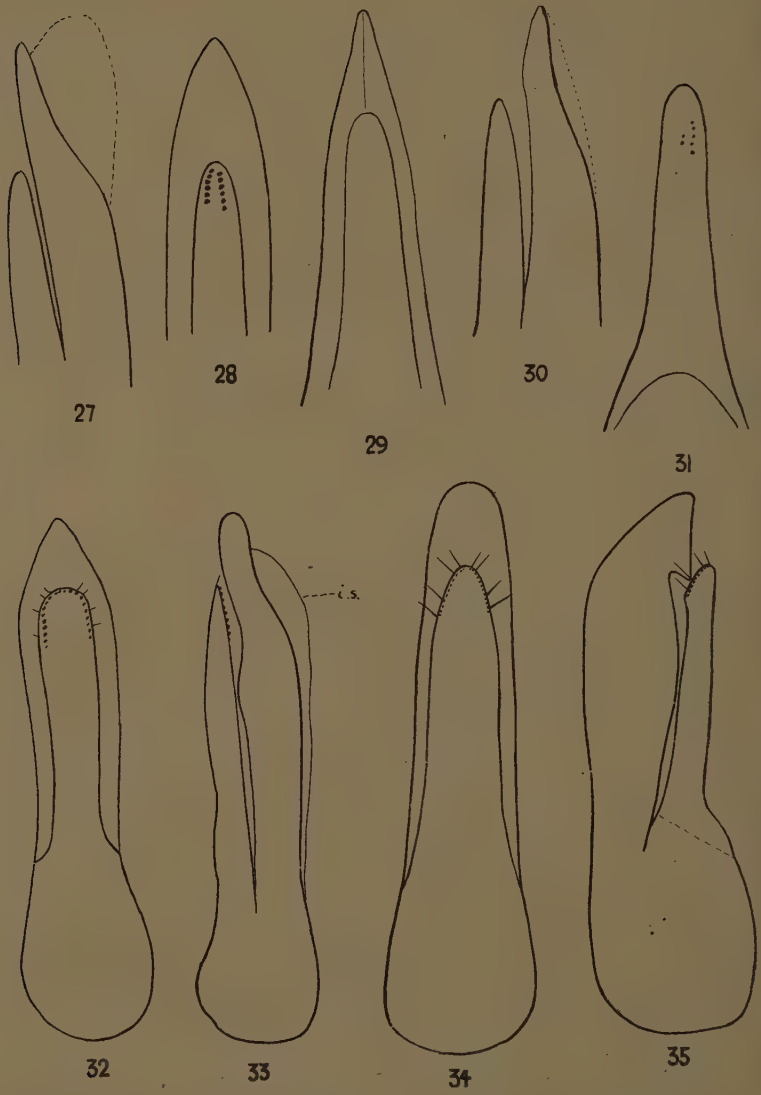
Black, shining, head and thorax very slightly aenescent, elytra green ; palpi reddish brown ; legs pitchy, tarsi reddish.

Head quadrate, much wider than long (3·3 : 2·5) ; front broad, but little produced before the eyes ; sides parallel ; posterior angles very obtusely rounded ; base broad, concave ; eyes very small and flat, occupying scarcely more than one-third of the lateral margins of the head. There is a faint longitudinal channel on the front of the head in the middle. In the unique type the interocular punctures differ both in number and disposition on the two sides of the head ; on the right there is a transverse row of three close, almost equidistant punctures, one being on the ocular margin ; on the left the marginal puncture is similar, but the other two are replaced by three, of which the first is a little more remote from the marginal puncture of the eye than the corresponding puncture on the other side, the other three are equidistant, but are placed a little nearer the centre of the head than the two on the opposite side ; it is impossible to say which is the normal number of punctures in the species, but at any rate there seems to be no reason to doubt that the interocular punctures consist of a transverse row of at least three fairly large, distinct punctures on each side of the head. The whole of the postocular region is covered with rather sparsely spaced fairly large punctures, which at the base of the head extend narrowly almost to the middle. Outstanding amongst these punctures are two on each side of the head, which with the second (from the eye) of the interocular punctures make two straight lines strongly converging towards the base of the head.

Palpi with the last segment scarcely longer than the penultimate.

Antennae wanting.

Thorax (male) as wide as the head, as long as broad, broadest in the middle, where the sides are distinctly but briefly rounded ; sides in front and behind sinuate ; anterior margin very straight ; anterior angles rectangular ; posterior angles rather marked, very obtuse ; base very strongly rounded. Discal series consisting of four moderate, nearly equidistant, punctures ; laterally with five other punctures in the anterior region. Ground sculpture, like that of the head, extremely close and fine.



FIGS. 27–35.—(27) *P. carpenteri* Bernhauer. Apex of aedeagus, lateral view. (28) *P. carpenteri*. Apex of aedeagus, upper view. (29) *P. phoculus* sp. n. Apex of aedeagus, upper view. (30) *P. phoculus*. Apex of aedeagus, lateral view. (31) *P. phoculus*. Paramere, inner face. (32) *P. jeanneli* Bernhauer. Aedeagus, upper view. (33) *P. jeanneli*. Aedeagus, lateral view. (34) *P. hirsutus* sp. n. Aedeagus, upper view. (35) *P. hirsutus*. Aedeagus, lateral view.

Scutellum very moderately and rather sparingly punctured.

Elytra broader than the thorax, distinctly wider than long, widened behind; punctuation rather irregular, not strong, rather close, finer and more sparing towards the shoulders.

Abdomen almost smooth, very finely and sparsely punctured.

Posterior tarsi mostly wanting, but the first segment is not very long, about double the length of the second.

Length: 14 mm.

Male: Anterior tarsi moderately dilated; eighth sternite rather long, broadly, not very deeply, triangularly emarginate. The aedeagus is of typical form, see figs. 29–31. The median lobe, however, is very feebly keeled down the centre of the apical portion on its inner face as far as the apex of the paramere; the paramere has a few irregular weak pegs in the centre at the apex; in fig. 30 the paramere has been pulled apart from the median lobe, and shows that the keel on the latter is almost invisible in the lateral view.

Type, male, unique, ABYSSINIA, without further data; in my collection.

20. *P. jeanneli* Bernhauer.

Bernhauer, 1939, *Mém. Mus. nat. Hist. nat. Paris* (N.S.) 9 : 82.

Black, with the head, thorax and elytra dark green, mandibles pitchy.

Head strongly transverse in both sexes (7 : 5); front concave between the antennae; eyes small, flat; sides behind eyes feebly rounded, almost parallel; eyes about equal to lateral margins behind eyes; posterior angles obtusely rounded; base concave. A strong longitudinal furrow in centre of head in front; three punctures close to base of each antenna; six or seven punctures along inner margin of each eye, four interocular larger punctures placed transversely, of which the inner puncture on each side of the head is about midway between the centre of the head and the inner margin of the eye; two other interocular punctures on each side behind these forming with them more or less a square; a second row of small punctures outside the marginal row along the inner margin of the eye; a number of punctures in the postocular region, and a distinct puncture on each side towards the centre of the head near the neck.

Antennae short; second segment as long as the third, shorter than the first; fourth longer than broad; fifth quadrate; sixth to tenth transverse but not strongly so.

Thorax not broader than head, broader than long (7 : 6); anterior margin truncate; anterior angles deflexed, rectangular if viewed from above; sides slightly converging in front and behind, rounded; posterior angles rounded with the base in a broad curve; discal series each consisting of four punctures; outside these series in the anterior half a series of two and a series of three punctures more or less parallel to the lateral margin.

Scutellum with a few fairly large shallow punctures.

Elytra slightly broader than the thorax, about as broad as long; punctuation fairly strong and diffuse.

Abdomen finely and diffusely punctured at the base and extreme apex of each segment.

Posterior tarsi with the first segment equal to the fifth, as long as second and third together.

Length: 14 mm.

Male: Anterior tarsi moderately dilated; sternite 8 emarginate, the emargination slightly bevelled; aedeagus, figs. 32, 33.

Type, male, MT. ELGON, iii.1934 (*R. H. Johnston*), 7000–9000 ft., in cow-dung, in British Museum (Natural History); WEST ABERDARES, over 9000 ft. iv.v.1934 (*H. A. J. Turner*); KINANGOP, x.1934 (*H. A. J. Turner*), in British Museum.

Note.—The green of the head and thorax is not obvious in one of the British Museum specimens; segments 1–4 of the anterior tarsi are usually lighter than the other tarsi.

21. **P. hirsutus** sp. n.

Black; head and thorax with a distinct purple reflection; elytra bright green with a bronze tint; legs, antennae and palpi blackish; elytra clothed with a long yellowish pubescence, hind body more scantily clothed with a greyish pubescence. Very shining, but abdomen duller.

Head (male) distinctly transverse, rectangular, about half as broad again as long; eyes large, but scarcely protruding at the sides, their longitudinal diameter being about two-thirds the length of the sides of the head. There is a large but very shallow depression in the middle in front. Head somewhat produced in front, anterior margin almost straight, sides behind eyes parallel, posterior angles obtuse. The anterior ocular punctures are placed at about one-third the inner margin of the eyes, each eye with another strong puncture at about two-thirds of this margin, and three more at the inner posterior angle. The interocular punctures are placed very far apart from one another, quite close to the anterior ocular punctures, and nearer to these than to the points of insertion of the antennae. There are two other large punctures on each side forming an oblique straight line with the second ocular puncture from the base of the head. A number of other less distinct punctures in the posterior angles of the head. All the punctures are setiferous, and there are two very long setae on each side of the head at the posterior angles.

Maxillary palpi with the last segment much longer than the penultimate.

Antennae about as long as the head and thorax together, the three basal segments glabrous, the rest very dull. All the segments are distinctly longer than broad, the second about half the length of the first, the third longer than the second, about two-thirds the length of the first, fourth to eighth about equal in length, ninth and tenth slighly shorter, distinctly but not very much longer than broad, eleventh about equal to the eighth, acuminately emarginate at the apex, but not strongly so.

Thorax scarcely wider than the head (male), quadrate, sides almost straight and parallel in front, slightly narrowed behind the middle, and then evenly rounded together with the base in a broad curve. The discal series consists of four punctures, the anterior puncture being further apart than the rest, the series slightly arcuate especially in front. There is a second series on each side, consisting of three punctures, strongly curved towards the discal series; two other punctures placed diagonally near the anterior angles. Marginal series consisting of about eight punctures. The punctures are set with long or very long setae.

Scutellum large, its length more than two-thirds that of the sutural margin of the elytra, finely punctured, clothed with yellowish pubescence.

Elytra slightly broader than the thorax, in length about equal to the thorax, broader than long; colour much as in *cupreonitens* Eppelsheim; puncturation fine, a little finer than in that species, clothed with fairly thick, long, yellowish pubescence; there are two very long lateral setae, one at the shoulder, the other at about two-thirds the length from the shoulder, on each side.

Abdomen with the basal segments shining, finely and sparingly punctured and pubescent; the puncturation is a little closer towards the apical segments; pubescence greyish; raised lines at base of segments straight.

Legs with the anterior tarsi strongly dilated in the male; posterior tarsi with the first segment long, equal to the fifth, but much shorter than the other three together; tibiae strongly spinose and pubescent.

Length: 10 mm.

Male: Eighth sternite broadly and triangularly emarginate at the apex, the emargination being almost in the form of an equilateral triangle, whose altitude equals one-quarter the length of the sternite.

LULUA: Kapanga, ix.1933 (*G. F. Overlaet*). 1 male. Type in the Musée du Congo Belge.

The species may easily be distinguished by its distinctive coloration from its allies. It comes near to *P. methneri* Bernhauer, from which it may also be distinguished by the more finely punctured elytra and more sparingly punctured basal segments of the abdomen.

The form of the aedeagus is shown in figs. 34, 35.

22. **Philonthus abdicans** sp. n.

This species is of the same narrow, parallel-sided form as *P. abyssinus* Fauvel, but differs in the colour of the elytra, etc.

Entirely black ; elytra bronze ; palpi and tarsi brownish.

Head quadrate, as long as broad, considerably produced before the eyes ; sides straight, parallel ; posterior angles very obtusely rounded ; base broad, concave. Eyes flat, very small, occupying about one-third of the lateral margins of the head. Median inter-ocular punctures not quite twice as distant from one another as from the marginal punctures of the eyes, which are situated right on the inner margin of the eyes. Another distinct large puncture on each side at the posterior angle of the eye, which together with two other large punctures on each side more towards the centre of the head, are arranged in an oblique line from the eye to the centre of the head near the base. The inner, i.e. posterior, pair of these punctures is as widely spaced as the median interocular punctures. The whole of the postocular region, extending round the base of the head towards the centre, is filled with large, sparingly placed punctures.

Mandibles with a very large, sharp tooth on the middle of their inner edge, very slender, long and sharp.

Antennae rather short, slender, feebly thickened towards the apex ; third segment longer than the second ; fourth very much longer than broad ; fourth to tenth markedly reduced in length, but the fourth to seventh all distinctly longer than broad ; ninth about as long as broad ; tenth a little transverse ; eleventh short.

Thorax a little broader than the head, and a little longer than broad ; anterior margin truncate ; anterior angles rectangular ; sides very feebly curved and very feebly narrowed anteriorly, almost straight and parallel ; posterior angles very broadly rounded with the base. Discal series consisting of four more or less equidistant moderate punctures, the fourth not much more distant from the base than from the third. Five other punctures laterally in the anterior half.

Scutellum rather small, moderately closely, not strongly, punctured.

Elytra at the side about as long as the thorax in the middle, a little broader together than long ; puncturation rather coarse and close ; pubescence rather close, whitish, not very long.

Abdomen moderately finely and sparingly punctured.

Posterior tarsi with the first segment much longer than the fifth, as long as the second and third together.

Length : 13 mm.

Male : Anterior tarsi only moderately dilated ; eighth sternite triangularly emarginate at apex.

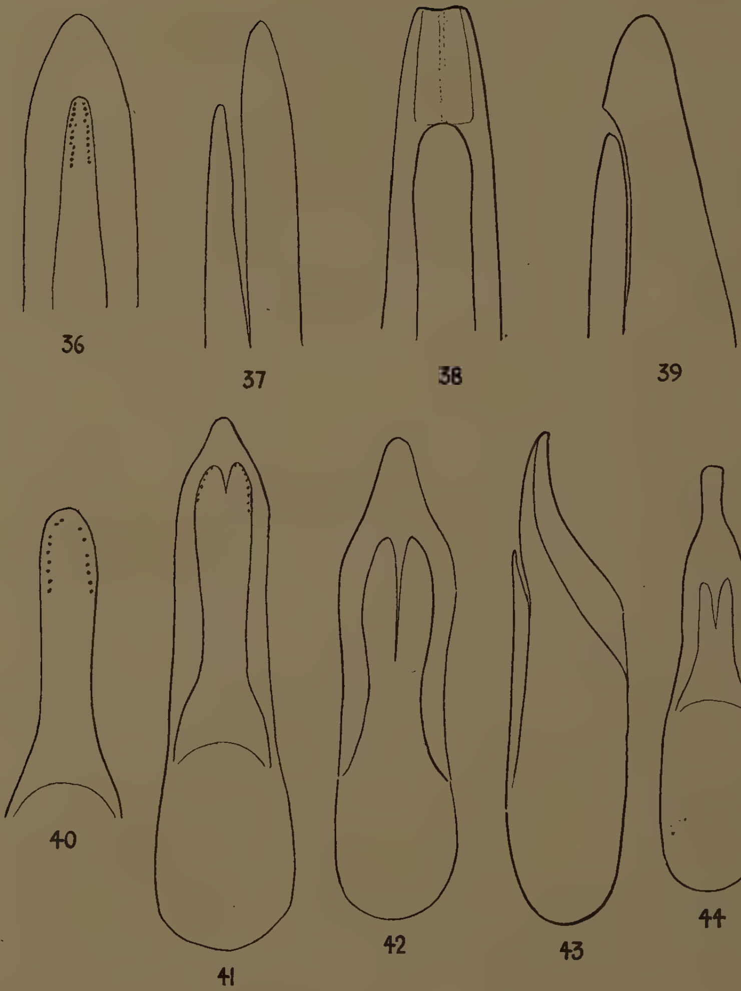
Type, male, unique, S. AFRICA, without further data, but probably from Cape Colony, in my collection.

The aedeagus is of typical form. (*See* figs. 36, 37.)

23. *P. natalensis* Boheman.

Boheman, 1848, *Ins. Caffr.* **1** : 278.
var. *vittatus* Roth, 1851, *Arch. Naturgesch.* **17** (1) : 118.

The aedeagus of this species is remarkable on account of the shape of the apex of the median lobe. Viewed from the side it shows a large hook, as do some other species ; but viewed from above, it will be seen that the hooked



Figs. 36–44.—(36) *P. abdicans* sp.n. Apex of aedeagus, upper view. (37) *P. abdicans.* Apex of aedeagus, lateral view. (38) *P. natalensis* Boheman. Apex of aedeagus, upper view. (39) *P. natalensis.* Apex of ædeagus, lateral view. (40) *P. natalensis.* Paramere, inner face. (41) *P. abyssinus* Fauvel. Aedeagus, upper view. (42) *P. pseudabyssinus* Tottenham. Aedeagus, upper view. (43) *P. pseudabyssinus.* Aedeagus lateral view. (44) *P. elgonensis* Tottenham. Aedeagus, upper view.

portion is elevated above the rest of the lobe in a raised surface, extending to the apex of the paramere, which surface is longitudinally impressed in the middle. The median lobe is also very slightly emarginate at the apex (viewed from above). The paramere is of the usual form. (*See* figs. 38–40.)

24. *P. abyssinus* Fauvel.

Fauvel, 1880–81, *Ann. Mus. stor. nat. Gen.* 16 : 203.

25. *P. pseudabyssinus* Tottenham.

Tottenham, 1940, *Ent. mon. Mag.* 76 : 148.

26. *P. elgonensis* Tottenham.

Tottenham, 1940, *op. cit.* : 149.

The differences between these three species are so slight that there would be little justification in regarding them as specifically distinct were it not for the marked differences in the male genitalia. These differences can be easily appreciated by reference to the figures—*abyssinus* Fauvel, fig. 41 ; *pseudabyssinus* Tottenham, figs. 42, 43 ; *elgonensis* Tottenham, figs. 44, 45.

27. **P. nimboides** sp. n.

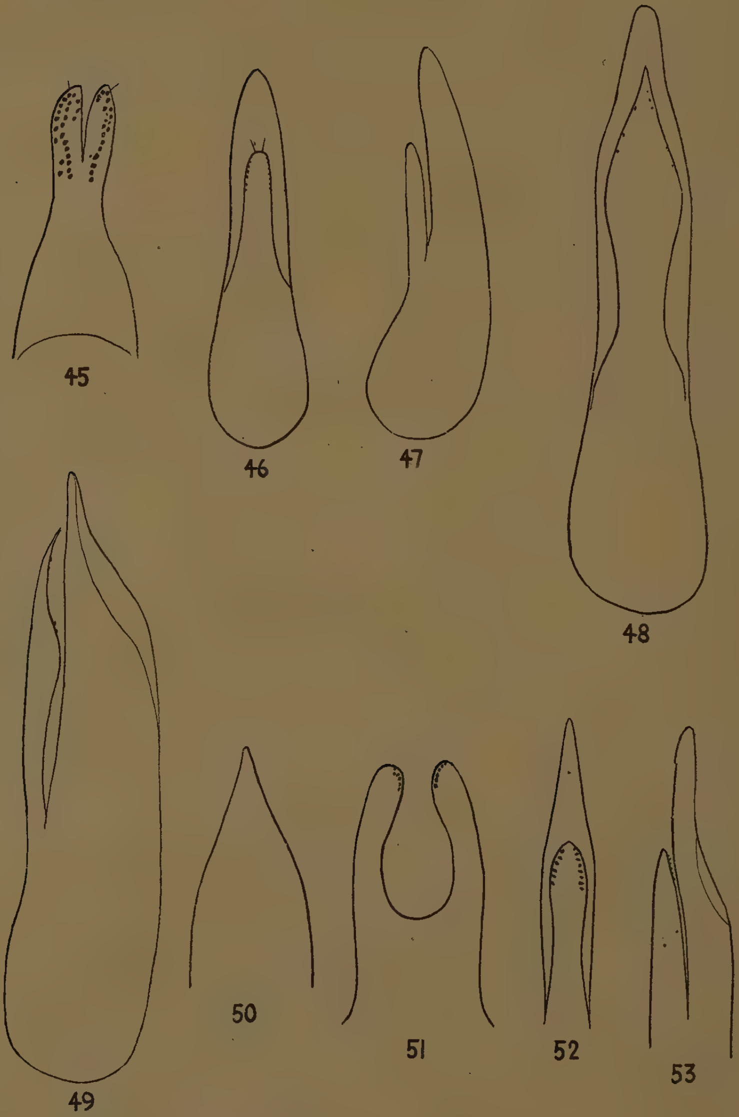
A large, black, depressed species, of conspicuous appearance, resembling a *Belonuchus*. Palpi red-brown ; legs, last segment of antennae, apical borders of abdominal segments brownish.

Head transverse in both sexes, very little produced before the eyes, anterior margin broad and straight. Eyes small ; sides of head behind eyes equal to about twice the longitudinal diameter of the eye. Sides of head parallel, posterior angles strongly rounded ; basal margin concave. Head in male about half as broad again as long, in female about one-third as broad again as long. Front of head broadly impressed, a large, deep, distinct circular depression in the middle, and on each side of this a less distinct impression containing the interocular puncture. The interocular punctures are large, widely separated, nearly twice as distant from one another as from the marginal ocular puncture, which is situated slightly anteriorly to them. Two other very large punctures level with the hind margin of the eye, placed much more widely apart, and two others towards the base but considerably distant from it, placed nearer together than are the interocular punctures. These six punctures, together with the anterior central depression form a circle. There are four other punctures at the inner posterior angle of each eye, and there is also a cluster of large punctures behind the eye.

Mandibles fairly long, outer edge straight in the basal half, then strongly curved ; inner edge strongly, bluntly toothed a little below the middle ; left mandible much more slender than the right.

Antennae long, the first three segments shining, the rest dull ; basal segments reddish at their extreme bases, the apical segments reddish ; second segment equal to the third, much shorter than the first ; fourth to sixth decreasing in length but longer than broad ; seventh quadrate ; eighth to tenth decreasing in length, transverse, but not strongly so in their widest aspect, eleventh short.

Thorax slightly broader than long ; anterior angles rectangular ; anterior margin rounded ; sides straight and slightly widened from the front to about the middle, then strongly narrowed and hollowed ; posterior angles broadly rounded with the base. Discal series slightly arcuate, the middle punctures being closer to the middle of the thorax than the anterior or posterior punctures ; series each consisting of four strong punctures, equidistant from one another, the first appreciably distant from the anterior margin ; usual five punctures in the anterior lateral region on each side.



Figs. 45–53.—(45) *P. elgonensis* Tottenham. Paramere, inner face. (46) *P. nimboides* sp. n. Aedeagus, upper view. (47) *P. nimboides*. Aedeagus, lateral view. (48) *P. aethiops* Bernhauer. Aedeagus, upper view. (49) *P. aethiops*. Aedeagus, lateral view. (50) *P. rhodesiae* sp. n. Apex of median lobe, inner face. (51) *P. rhodesiae*. Apex of paramere, inner face. (52) *P. praetor* sp. n. Apex of aedeagus, upper view. (53) *P. praetor*. Apex of aedeagus, lateral view.

Elytra together as wide as the thorax and slightly longer than broad; puncturation fairly strong, fairly close, even; pubescence short, scanty, greyish.

Scutellum with fairly close and fine puncturation.

Abdomen smooth, shining, very scarcely and very finely punctured, a little more at the bases of the segments than at the apices; pubescence scarce, greyish.

Legs with the anterior tarsi very slightly dilated in both sexes; anterior tibiae strongly pubescent, with two short, black spurs on basal half of the anterior outer edge, about eight on posterior outer edge, two on posterior inner edge; apical spurs reddish, the anterior spur much longer than the posterior; intermediate and posterior tibiae closely pubescent with rows of four or five long black spurs on the edges, posterior apical spur longer than the anterior spur on each; posterior tarsi shorter than the tibiae, with first segment fairly long, equal to the fifth, slightly longer than second and third together, but shorter than the second, third and fourth together.

Length: 15 mm.

Male: Aedeagus, figs. 46, 47.

Type, male, S. Rhodesia: Vumbu Mts., alt. 5700 ft., ii.1926.
Type, female, S. Rhodesia: Cloudlands, Vumbu Mts., alt. 6000 ft., iv.1923.
Types in the Rhodesian Museum.

28. *P. aethiops* Bernhauer.

Bernhauer, 1915, *Ann. Mus. nat. Hung.* **13**: 137.

The aedeagus possesses an unusual form of paramere, which is widely dilated in the apical portion, like so many other species, but is produced at the apex into an exceptionally long point. The pegs appear to be few in number and arranged at intervals along the outer margins anterior to the widest part of the paramere. Viewed laterally the paramere is narrowed in a curve on its inner face to a slender point. (Figs. 48, 49.)

Section B.

Having included the larger black species in Section A, the present section contains mostly small or moderate sized species.

1. Elytra entirely red; size moderately large, about 12 mm. 29. **rhodesiae** sp. n.
 Elytra not entirely red . . . . 2.
2. Elytra red, with suture and a longitudinal lateral stripe dark
 30. **praetor** sp. n.
 Elytra black, with an oblique red stripe on each . . . . 3.
 Elytra otherwise coloured . . . . 4.
3. Elytra dilated behind, wider than thorax; basal segments of abdomen "sat dense" punctured . . . . *vittiger* Fauvel.
 Elytra widest in middle, narrowed before and behind, not appreciably wider than thorax; abdomen almost smooth . . 31. **rubrovittatus** sp. n.
4. Elytra blue or blue-green or green-bronze . . . . 5.
 Elytra otherwise coloured . . . . 7.
5. Elytra dark green-bronze; legs yellow; thorax long and narrow
 motoensis Cameron.
 Elytra blue or blue-green . . . . 6.
6. Elytra metallic blue-green; femora brown; thorax broader in proportion to elytra . . . . 32. *uelensis* Bernhauer.
 Elytra dark metallic blue; femora black; thorax narrower in proportion to elytra . . . . 33. *paederomimus* Eppelsheim.

7. Thorax, elytra and abdomen brown . . . . . . 8.
Insect otherwise coloured . . . . . . 9.
8. Head black . . . . . . 34. *volvulus* Bernhauer.
Head brown . . . . . . 35. *rufescens* Bernhauer.
9. Head strongly and closely punctured over the whole basal area, a large space on vertex only smooth . . . . . . 36. **cribricephalicus** sp. n.
Head normally punctured . . . . . . 10.
10. Anterior tibiae with large strongly hooked spur at apex 37. **unguicularis** sp. n.
Anterior tibiae with normal spurs . . . . . . 11.
11. Elytra with apical part broadly testaceous or reddish . . . . . . 12.
Elytra otherwise coloured . . . . . . 13.
12. Size larger, 8 mm., broader; anterior angles of thorax upturned and broad; elytra transverse, strongly and diffusely punctured; abdomen finely and diffusely punctured . . . 38. *bicoloripennis* Bernhauer.
Size smaller, 5 mm., narrower; anterior angles of thorax not marked, deflexed; elytra longer than broad, moderately finely and moderately closely punctured; abdomen very closely and very finely punctured . . . . . . 39. **kashituensis** sp. n.
13. Elytra with the apical external angles broadly pale testaceous; size very small, 4 mm. . . . . . . 40. **clambus** sp. n.
Elytra otherwise coloured . . . . . . 14.
14. Abdomen quite or very nearly impunctate . . . . . . 15.
Abdomen rather closely or very closely punctured . . . . . . 17.
15. Head transverse oval; antennal segments distinctly longer than broad; thorax wider; paramere with long tooth-like pegs inclined outwardly along the apical margins of inner face 41. *rudipennis* Fauvel.
Head rounded, not transverse; penultimate antennal segments not or scarcely longer than broad; thorax narrower . . . . . . 16.
16. First segment of antennae light; legs light, tibiae slightly infuscate; abdomen iridescent . . . . . . 42. **iridescens** sp. n.
First segment of antennae black; legs dark, very infuscate; abdomen black . . . . . . *parciventris* Bernhauer.
17. Elytra with sides, apical margins and suture narrowly testaceous . 18.
Elytra otherwise coloured . . . . . . 20.
18. Size much larger, 10 mm.; head strongly transverse; suture of elytra broadly reddish testaceous (apical margins and sides also distinctly testaceous); puncturation of elytra much stronger and more sparing 43. *cinctus* Fauvel.
Size smaller, 7 mm. or less; head not or only a little transverse; testaceous border very narrow; puncturation of elytra much closer and finer . . . . . . 19.
19. Head not or scarcely transverse; elytra brownish black, more sparingly and less finely punctured; abdomen not iridescent, less closely and less finely punctured . . . . . . 44. *marginipennis* Wollaston.
Head transverse; elytra with a distinct greenish tint, more closely and more finely punctured; abdomen iridescent, more closely and more finely punctured . . . . . . 45. *parvicornis* Fauvel.
20. Size larger, 8 mm.; elytra more or less shining; abdomen shining; antennae dark, first segment lighter beneath . *somaliensis* Eppelsheim.
Size smaller, 6·5 mm.; elytra and abdomen duller; antennae with basal segments lighter . . . . . . 46. *robusticornis* Bernhauer.

(*N.B.*—This key covers a little over half the known species in the group.)

29. **P. rhodesiae** sp. n.

Distinct by reason of its fairly large size, red elytra and compact build.

Black ; elytra red ; antennae, mouth parts and legs pitchy red.

Head broader than long (5 : 4) ; front slightly rounded ; sides straight, almost parallel ; eyes occupying a little more than half the sides of the head ; posterior angles broadly rounded ; a slight depression between the eyes ; median pair of interocular punctures more than twice as distant from one another as from the marginal puncture of the eye ; an oblique row of three equidistant punctures on each side of the head between the hind margin of the eye and the neck.

Antennae with the first segment short ; second about two-thirds the length of the first ; third as long as the second ; fourth to tenth transverse, the fourth scarcely, the tenth strongly so (about twice as broad as long).

Thorax quadrate ; anterior margin truncate ; anterior angles rectangularly rounded, explanate ; sides slightly sinuate and convex anteriorly, parallel in the basal half ; posterior angles rounded with the base. Discal series consisting of four moderate punctures equidistant from one another except the fourth, which is a little nearer ; laterally with the usual punctures.

Scutellum moderately closely and finely punctured.

Elytra quadrate, slightly wider than the thorax, moderately closely, finely and shallowly punctured ; pubescence scanty, yellowish.

Abdomen very closely and finely punctured throughout and dull, except the last segment, which is moderately and sparsely punctured and shining.

Posterior tarsi with the first segment equal to the second and third together, barely as long as the fifth.

Length : 12 mm.

Male : Anterior tarsi dilated ; eighth sternite broadly, triangularly excised on its apical margin, the apical part of the triangle with a membrane.

The aedeagus, figs. 50, 51, is distinct. The median lobe is strongly narrowed and pointed at the apex ; the paramere is furcate, with the two branches approaching one another apically ; the pegs appear to be few in number and arranged in a row along the inner margin of each branch at the apex.

N.W. Rhodesia : Kashitu, N. of Broken Hill, ii.1915 (*H. C. Dollman*). Type and a number of other specimens from the same locality in the British Museum (Natural History).

30. **P. praetor** sp. n.

It is with some hesitation that I describe this insect as a new species. It would appear to be very closely related to *usambaricus* Bernhauer, judging from the description of that species, differing in a few minor points. The elytra of *praetor*, however, can certainly not be described as " hell rötlichgelb " ; also Bernhauer, although he was describing a male, failed to figure or even mention the aedeagus. Less confusion will be caused by describing it as new than by making a mistaken guess as to its identity with Bernhauer's species.

Amongst the four-punctate species, easily recognized by the colour of the elytra.

Black ; elytra dark brownish red, with the sutural region and a lateral patch on each elytron black ; the sutural dark mark is in the form of a triangle, whose base extends along the bases of the elytra and whose apex reaches the apical end of the suture ; each lateral patch of black is parallel to the lateral margin of the elytron, extending from almost the apex to about two-thirds the length of the elytron to the shoulder, and also extending laterally on the reflexed portion but not quite reaching its margin ; the antennae are black, with the first two segments brownish ; femora and tarsi reddish testaceous ; abdomen a little iridescent and with the apical margins of tergite 6 narrowly and 7 and 8 broadly reddish brown.

Head transverse oval, very flatly rounded in front, sides behind eyes feebly convergent posteriorly, posterior angles very obtusely rounded ; eyes about equal to the lateral margins of the head behind the eyes, measured to the bristle. Antennae a little shorter than head and thorax together ; third segment longer than second, fourth and fifth distinctly longer than broad, fourth to tenth decreasing in length, the tenth being feebly transverse, eleventh shorter than the two preceding together ; segments four to ten not increasing in width. The inter-ocular punctures are very widely distant from one another, each being rather close to the anterior marginal puncture of the eye ; two other punctures close to the margin of the eye near its inner hind angle ; a few other scattered punctures in the postocular region.

Thorax slightly transverse, with all the angles obtusely rounded ; in front as wide as the head, behind considerably wider, sides very feebly rounded. Discal series each consisting of four punctures, of which the first is distinctly more external than the rest, and the second and third are more widely distant from each other than from one and four ; usual lateral punctures feeble.

Scutellum fairly closely and moderately strongly punctured.

Elytra slightly wider than the thorax at its greatest breadth, together broader than long ; rather evenly, closely, moderately strongly punctured ; pubescence short.

Abdomen smooth and shining with very fine and sparing puncturation, especially at the bases and central regions of each segment ; the punctures show a tendency to fall into two or three transverse rows on each segment, one close to apical margin, the other one or two across the middle ; tergite eight is much more evenly, though equally finely but more sparingly punctured throughout.

Legs with the tarsi rather short, the posterior tarsus shorter than the tibiae, with the first segment longer than the fifth and about equal to the second and third together.

Length : 9 mm.

Male : Eighth sternite triangularly, not very deeply emarginate ; aedeagus, see figs. 52, 53.

Type, unique male, S. RHODESIA : Bulawayo, 28.xii.1924, in my collection.

31. **P. rubrovittatus** sp. n.

Black ; mouth parts brown ; thorax brownish black ; each elytron with a large red fascia extending obliquely from the shoulder to the inner apical angle ; abdomen rather iridescent, shining ; legs reddish brown, tibiae a little darker.

Head a little broader than long (5 : 5·4) ; front considerably produced and rounded ; eyes very flat, longer than the side of the head behind the eye (16 : 11) ; sides very feebly rounded, almost parallel, then strongly convergent and straight from the bristle to the neck ; base broad, straight. Median interocular punctures very small, very widely distant from one another, and very near the marginal punctures of the eyes ; a few similar punctures in the postocular region ; ground sculpture very close and fine, transverse.

Antennae shorter than the head and thorax together ; third segment a little longer than the second ; fourth about half as long again as broad ; fourth to tenth decreasing in length, tenth quadrate ; eleventh much longer than the tenth ; none of the segments transverse.

Thorax distinctly wider than the head, about half as long as broad ; truncate in front ; anterior angles depressed, rather prominently rounded ; sides nearly straight, divergent posteriorly ; base broader than the apex (7·5 : 6·3) ; posterior angles widely rounded with the base. Discal series each consisting of four equidistant, widely spaced, small punctures.

Scutellum finely, not closely, punctured.

Elytra in the middle a little wider than the thorax (8 : 7·5) and about as long, together wider than long (8 : 7·5), at base distinctly narrower than the thorax; rather closely, moderately finely and asperately punctured.

Abdomen almost smooth, with a few fine setiferous punctures transversely placed on each segment.

Posterior tarsi long, first segment about equal to the fifth, and equal to the second and third together.

Length: 9 mm.

Type, unique, female, in the Musée du Congo Belge. KIVU: Lulenga, 14.xi.1925 (*Dr. H. Schouteden*).

This species is very like the description of *P. vittiger* Fauvel, but in that species the elytra are said to be wider than the thorax, somewhat dilated from base to apex, whereas in the new species they are at base narrower than the thorax, nearly parallel-sided, slightly rounded, widened from base to middle and then distinctly narrowed to apex. *P. vittiger* is described as having the basal segments of the abdomen " sat dense " punctured, whereas in *rubrovittatus* they are almost smooth like the rest of the abdomen.

32. *P. uelensis* Bernhauer.

Bernhauer, 1928, *Wien ent. Ztg.* 45 : 112.

The aedeagus of this species is very distinct by the form of the paramere, which in the lateral view appears to have a large hooked apical portion (fig. 54) and in the upper view is very widely dilated in the apical region (fig. 55). In the latter respect it somewhat recalls the paramere of *combustus* Fauvel (fig. 92).

According to Bernhauer the species is closely related to *P. bottegoi* Eppelsheim (1895, *Ann. Mus. stor. nat. Genova* **35** : 207), but is smaller and more slender, with smaller and narrower head, and longer and narrower thorax. The head and thorax also are quite black, instead of being iridescent (" sericeo-submicantibus ") as in *bottegoi*.

33. *P. paederomimus* Eppelsheim.

Eppelsheim, 1895, *Ann. Mus. stor. nat. Genova* 35 : 206.

Apart from its paederoid appearance, this species is remarkable for the structure of the aedeagus. The paramere, viewed laterally, is abruptly narrowed for the apical half, the outer margin being continuous and nearly straight, the inner margin being sharply bent away from the median lobe at about the middle. Viewed from above, or from its inner face, there is a distinct angular widening near the middle, which appears to have a dark ridge across its widest part. So far as I can make out, this ridge is formed by a row of contiguous pegs. There are no pegs near the apex. (*See* figs. 56–58.)

34. *P. volvulus* Bernhauer.

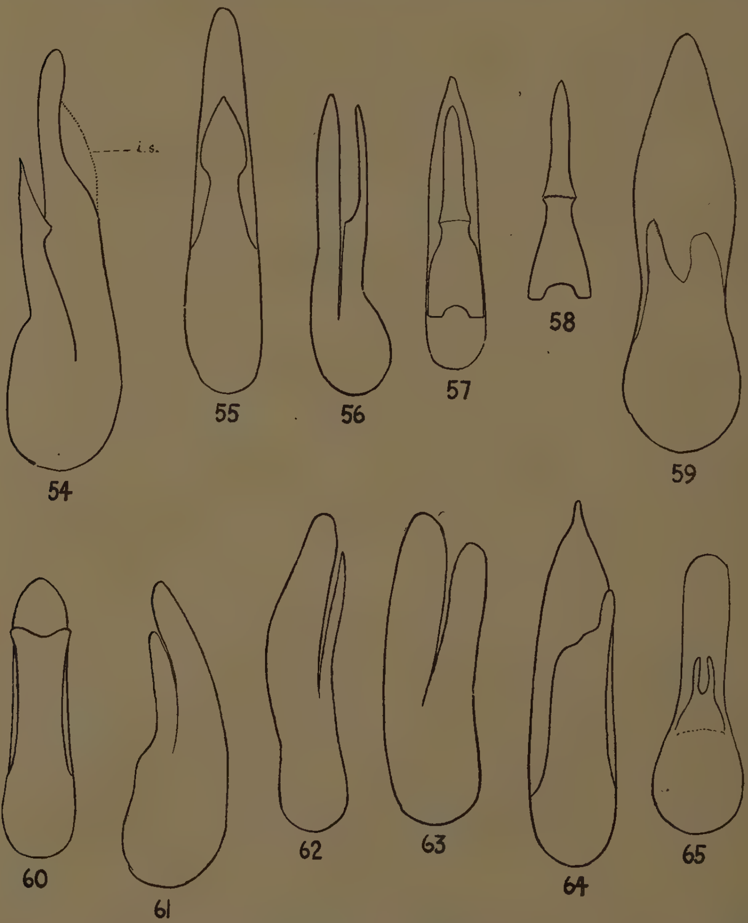
Bernhauer, 1932, *Rev. Zool.-Bot. afr.* 22 : 151.

The only specimen I have seen of this species appeared to be rather immature; the paramere in this specimen was asymmetrical and furcate. In the upper view of the aedeagus, the left fork of the paramere was distinct and studded with a few fine pegs near the apex on its inner margin, the right fork was ill-defined, but obviously smaller than the left and without pegs; the outline of this part in the diagram must only be regarded as approximate. (Fig. 59).

35. *P. rufescens* Bernhauer.

Bernhauer, 1915, *Ergebn. Hamburg. D.S.W. Afr. Stud. Reise* **7** : 319.

This species, which may be known by its more or less uniform brown colour and small size, differs from the previous species in not having a black head, and in the very different form of the aedeagus. The paramere is relatively long,



FIGS. 54–65.—(54) *P. uelensis* Bernhauer. Aedeagus, lateral view. (55) *P. uelensis.* Aedeagus, upper view. (56) *P. paederomimus* Eppelsheim. Aedeagus, lateral view. (57) *P. paederomimus.* Aedeagus, upper view. (58) *P. paederomimus.* Paramere, inner face. (59) *P. volvulus* Bernhauer. Aedeagus, upper view. (60) *P. rufescens* Bernhauer. Aedeagus, upper view. (61) *P. rufescens.* Aedeagus, lateral view. (62) *P. cribricephalicus* sp. n. Aedeagus, lateral view. (63) *P. cribricephalicus.* Aedeagus, showing paramere outer face. (N.B. the median lobe is twisted and shows more or less lateral view.) (64) *P. bicoloripennis* Bernhauer. Aedeagus, upper view. (65) *P. kashituensis* sp. n. Aedeagus, upper view.

nearly as broad as the median lobe for the greater part of its length, a little broader at its extreme apex; its apical margin is emarginate in a broad curve. It somewhat recalls the aedeagus of the European *P. fimetarius* Gravenhorst. (Figs. 60, 61.)

36. **P. cribricephalicus** sp. n. ✓

In the British Museum this species stands over the name *cribriceps* Bernhauer, which is apparently a manuscript name, and cannot be applied to the present species, since Bernhauer has already described a South American species under this name (1921, *Wien ent. Ztg.* **38** : 105).

Pitchy; elytra with a green metallic tint; legs testaceous, with margin of tibiae infuscate; palpi brownish testaceous; antennae black with the second and third segments rather brownish and with the first and eleventh segments brownish testaceous.

Head broader than long, widest in front; very little produced in front of the eyes; eyes small, occupying not more than half the sides of the head; sides nearly straight, convergent posteriorly; posterior angles obtusely rounded; base straight; slightly depressed on the vertex; median interocular punctures nearly as close to each other as to the marginal pair; the whole of the region between them and the eye, the postocular region and the basal region moderately and distinctly punctured, leaving only a very small smooth space in the middle of the head.

Antennae long and slender; all the segments longer than broad; third segment a little longer than the second; fourth nearly twice as long as broad; fifth to tenth decreasing in length, but the tenth still distinctly longer than broad; eleventh short, about equal to the seventh.

Thorax much longer than the head and much longer than broad; narrower than the head; widest in front, narrow behind, rather cordate; anterior margin slightly rounded, anterior angles obtusely rounded; sides nearly straight, slightly sinuate in basal half; posterior angles obtusely rounded; base feebly rounded. Discal series consisting of four moderate, equidistant, widely spaced punctures; five other lateral punctures in addition to the usual marginal punctures.

Scutellum more closely and finely punctured than the elytra.

Elytra as long as the thorax, wider than long, much wider than the thorax; punctuation close and fine; pubescence fine, grey.

Abdomen more finely punctured than the elytra, and more sparsely, especially at the apex of each segment.

Legs long and slender; posterior tarsi shorter than the tibiae; first segment nearly equal to the fifth, as long as the three following together.

Length: 7 mm.

The lateral view of the aedeagus is shown in fig. 62; fig. 63 shows the median lobe more or less laterally, but shows the outline of the paramere as viewed from above.

Type in British Museum. MASHONALAND: Salisbury (Marshall coll.); also from NATAL: Frere (Marshall coll.) and NATAL: Kloof, viii.1926, 1500 ft. (*R. E. Turner*).

37. **P. unguicularis** sp. n. ✓

A medium-sized, parallel-sided, depressed species, somewhat of the build of *P. rectangulus* Sharp, remarkable by the strongly hooked apical spur of the anterior tibiae.

Black; palpi and legs red; antennae red except for the middle segments which are fuscous; last segment of abdomen and the apical margin of the preceding one lighter; head and thorax shining, elytra and abdomen less so.

Head large, transverse, considerably produced and rounded in front; sides behind the eyes parallel, about equal in length to the longitudinal diameter of the eye; posterior angles rounded, slightly obtuse, almost right angles; basal margin straight. There is a large, very deep, circular depression near the front margin, but since this is situated in the unique type distinctly to the left side, it is impossible to say to what extent this depression is normal. A row of five or six punctures against the inner margin of the eye. The median interocular punctures are as close to one another as to the margin of the eye. A number of large punctures in the posterior angles of the head and along the posterior margin. There are also numerous distinct but small and fine punctures scattered all over the surface of the head.

Maxillary palpi with the apical segment much longer than the preceding, straight on the outer margin, strongly narrowed in a curve on the inner margin, acuminate at the apex.

Labial palpi with the last segment very large and long, oval.

Antennae with all the segments as long as or longer than broad; second half the length of the first; third longer than second; fourth distinctly longer than broad; fifth to tenth decreasing in length, the ninth and tenth being quadrate; eleventh short, but longer than broad, globular, but little acuminate.

Thorax broader than the head (female), considerably longer than broad, parallel-sided, rounded in front and behind, all the angles broadly and evenly rounded. The left discal series consists of four widely spaced punctures, in which the second and third are more widely spaced than the others; the right discal series has the third puncture missing; several other punctures towards the sides in front in addition to the usual marginal puntures. Like the head, the thorax is covered with small scattered punctures.

Scutellum fairly smooth, with several moderate punctures.

Elytra about as long and broad as the thorax, very closely, deeply and evenly punctured.

Abdomen moderately closely and moderately strongly punctured at the base, but much less strongly than the elytra; the punctures become finer and more sparing towards the apex; pubescence scanty, short and brownish.

Legs slender, tibiae scantily pubescent with a few small slender spines; apical spurs very short; anterior tibiae with the outer spur very long and strongly hooked; the anterior tibiae short and strongly dilated. Tarsi long and slender; anterior tarsi slightly longer than the tibiae, squamose beneath; intermediate tarsi distinctly longer than the tibiae; posterior tarsi about equal to the tibiae; basal segment in all the tibiae about equal to the last, but less than the other three segments together.

Length: 10 mm.

Type, unique, female, EQUATEUR: Flandria, iii–iv. 1929 (*R. P. Hulstaert*), in the Musée du Congo Belge.

38. *P. bicoloripennis* Bernhauer.

Bernhauer, 1915, *Verh. zool.-bot. Ges. Wien* **65**: 302.

This species, for which Bernhauer created a new subgenus, *Pseudophilonthus*, on account of the form of the sidelines of the thorax and of the temples, also has an abnormal aedeagus, as may be seen from fig. 64. The paramere, directed to the right side of the median lobe (viewed from above) is reminiscent of the paramere of *P. longicornis* Stephens and its allies, but differs in being broad for the greater part of its length; the apical portion of the median lobe, also, is entirely different.

39. **P. kashituensis** sp. n.

The build of *P. ochripennis* Cameron, but very much smaller and differently coloured.

Head black; thorax brownish black; elytra testaceous, with the basal margin, scutellary region and suture dark brown; abdomen blackish, rather dull, with the apical margins of the segments (especially the apical segments) reddish brown; mouth parts reddish brown; antennae pitchy with the eleventh and the first three segments testaceous; legs testaceous, of the same colour as the elytra.

Head oval, broader than long (3·7 : 3), very flatly rounded in front; sides feebly rounded, parallel, then very obtusely rounded to the neck; base feebly concave; eyes large, more than twice as long as the sides behind the eyes measured to the bristle (8 : 3); median interocular punctures widely distant from one another, three times as far apart as they are distant from the marginal punctures of the eyes; another pair of punctures, still more widely distant from one another and closer to another distinct marginal puncture of the eye, situated about two-thirds the length of the eye; several distinct punctures in the postocular region.

Antennae short and stout, about as long as head and thorax together; second and third segments nearly equal, not much shorter than the first; fourth to tenth increasing gradually in width, all strongly transverse; eleventh about as long as the two preceding together.

Thorax as wide as the head, quadrate, about as long as broad; anterior margin truncate; anterior angles rectangular; sides straight, almost parallel, very feebly divergent posteriorly; posterior angles very broadly rounded with the base. Discal series consisting of four moderate, nearly equidistant punctures, the first two being closer together and the second two wider apart than the last two; laterally with five other punctures; ground sculpture rather strong, very oblique, but less so, and less regular in direction than the ground sculpture of the head.

Scutellum finely, not closely, punctured.

Elytra as long as wide, a little wider than the thorax, parallel-sided; puncturation only moderately close and fine, a little closer, stronger and more irregular in the posterior angles; pubescence short, light.

Abdomen very finely and closely punctured and pubescent.

Legs short; posterior tarsi as long as the tibiae; first segment as long as the fifth, and about equal to the second and third together.

Length: 5·5 mm.

N.W. RHODESIA: Kashitu, 25.iii.1915 (*H. C. Dollman*).

Type and seven other specimens from the same locality in the British Museum (Natural History).

I have retained Bernhauer's MS. name for this species, but I have seen another specimen of the same species in the Belgian Congo Museum, which was submitted to me without a name, but which bore a label "n. sp." in what I believe to be Bernhauer's handwriting. This specimen is from HAUT-UELE: Moto, 1923 (*L. Burgeon*).

There is nothing remarkable about the aedeagus, fig. 65, but it is interesting to note its general resemblance to such species as the European *salinus* Kiesenwetter and some North American species, none of which are close allies of the present species.

40. **P. clambus** sp. n.

Black; apical angles and reflexed margins of the elytra testaceous; antennae black with the first segment brown; legs brown, tarsi lighter.

Head roundish, slightly transverse; eyes flat, more than twice the length of the lateral margins of the head behind the eyes (measured to the bristle) (12 : 5); front feebly rounded; sides behind eyes nearly straight and parallel as far as the bristle, then strongly rounded to the neck.

Antennae short; third segment nearly as long as the second, about two-thirds the length of the first; fourth a little longer than broad; fifth as long as broad; sixth to tenth transverse; eleventh shorter than the two preceding together; segments five to ten of about equal width.

Thorax in front as wide as the head, considerably widened behind; anterior margin truncate; anterior angles obtusely rounded; sides nearly straight; posterior angles rounded with the base in a big curve; dorsal series consisting of four fairly strong, equidistant punctures; laterally with two punctures in an oblique line on each side, and one in each anterior angle.

Elytra scarcely wider than the thorax, broader than long (9 : 7); apical angles slightly dilated; puncturation moderately fine, irregular; pubescence long and fine.

Abdomen closely, finely punctured and pubescent.

Posterior tarsi with the first segment a little shorter than the fifth, which is about equal to the second and third together.

Length: 4 mm.

Male: The form of the aedeagus is shown in figs. 66, 67.

Type, unique, S. RHODESIA (*R. H. R. Stevenson*), in my collection.

41. *P. rudipennis* Fauvel.

Fauvel, 1907, *Rev. Ent.* **26** : 41.

The specimen from which the figures of the aedeagus are drawn is in the British Museum and bears a label "*rudipennis* Fauv. var ?". The paramere is unlike that of any other species known to me, by reason of the very large tooth-like pegs which stand out, being outwardly directed, and are visible when the aedeagus is viewed from above, as well as when viewed laterally. (Figs. 68, 69.)

42. **P. iridescens** sp. n.

Black, very shining; abdomen with a strong blue-violet reflection at the sides; antennae black with the first segment and base of the second brown; legs light brown, with anterior and middle tibiae infuscate.

Head round, as long as broad; front a little produced and flat in the centre; sides behind eyes rounded to base; base concave; eyes occupying about half the sides of the head; a small circular depression on the vertex a little behind the antennae; three punctures along the inner margin of each eye; interocular punctures very close to the first of these; very few small punctures in the postocular region.

Antennae scarcely reaching base of thorax, and scarcely thickened towards apex; second segment as long as the third; fourth to tenth decreasing in length; fourth to seventh longer than broad; eighth quadrate; ninth and tenth feebly transverse; eleventh moderate.

Thorax anteriorly as wide as head, much widened behind, longer than broad; anterior margin truncate; sides nearly straight; posterior angles forming a large continuous curve with the base; discal series each consisting of four moderately large, shallow punctures; lateral series of two placed obliquely, and two others in the anterior angle.

Scutellum moderately and closely punctured towards the apex.

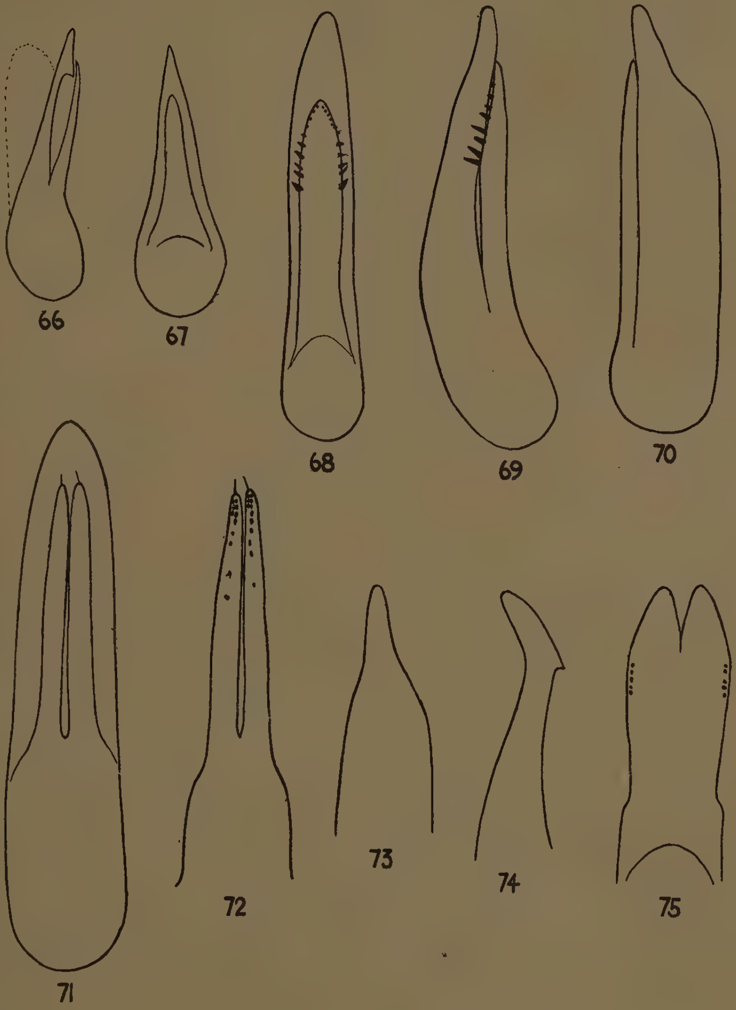
Elytra not wider than the thorax, parallel-sided, longer than broad; very strongly and closely punctured; pubescence light, scanty.

Abdomen very finely and very diffusely punctured, almost smooth; pubescence scanty, long, light.

Posterior tarsi with the first segment a little longer than the fifth, about equal to the second and third together.

Length: 8 mm.

ZULULAND: Eshowe, 1–22.vi.1926 (*R. E. Turner*), type in the British Museum (Natural History). Another specimen from the same locality, vii.1926.



FIGS. 66–75.—(66) *P. clambus* sp. n. Aedeagus, lateral view. (67) *P. clambus.* Aedeagus, upper view. (68) *P. rudipennis* Fauvel. Aedeagus, upper view. (69) *P. rudipennis.* Aedeagus, lateral view. (70) *P. cinctus* Fauvel. Aedeagus, lateral view. (71) *P. cinctus.* Aedeagus, upper view. (72) *P. cinctus.* Paramere, inner face. (73) *P. marginipennis* Wollaston. Apex of median lobe, upper face. (74) *P. marginipennis.* Apex of median lobe, lateral view. (75) *P. marginipennis.* Paramere, inner face.

43. *P. cinctus* Fauvel.

Fauvel, 1905, *Rev. Ent.* **24** : 140.

The most noticeable feature about the aedeagus of this species is the long, deeply divided paramere. The pegs, judging from the single specimen examined, are closer at the apex, where they are in double rows and become much more widely spaced and irregular further down each prong of the paramere. (Figs. 70–72.)

44. *P. marginipennis* Wollaston.

Wollaston, 1867, *Col. Hesperid.* : 236.

The aedeagus is characterized by the outwardly bent hooked apex of the median lobe (viewed laterally) (fig. 74), by the median lobe being prolonged and narrowed at the apex (viewed from above) (fig. 73) and by the broad furcate paramere on which the pegs are situated below the furcation in two rows close to the outer margins, there being five pegs in each row (fig. 75); the exact number of pegs probably varies somewhat.

45. *P. parvicornis* Fauvel.

Fauvel, 1907, *Rev. Ent.* **26** : 40.

The aedeagus of this species is very typical in form; however, the apex of the median lobe is rather unusually narrowed in the lateral view, and the paramere has a very long row of pegs on each of its outer margins in the apical portion; the paramere is also a little constricted and then widened towards the base. (Figs. 76–78.)

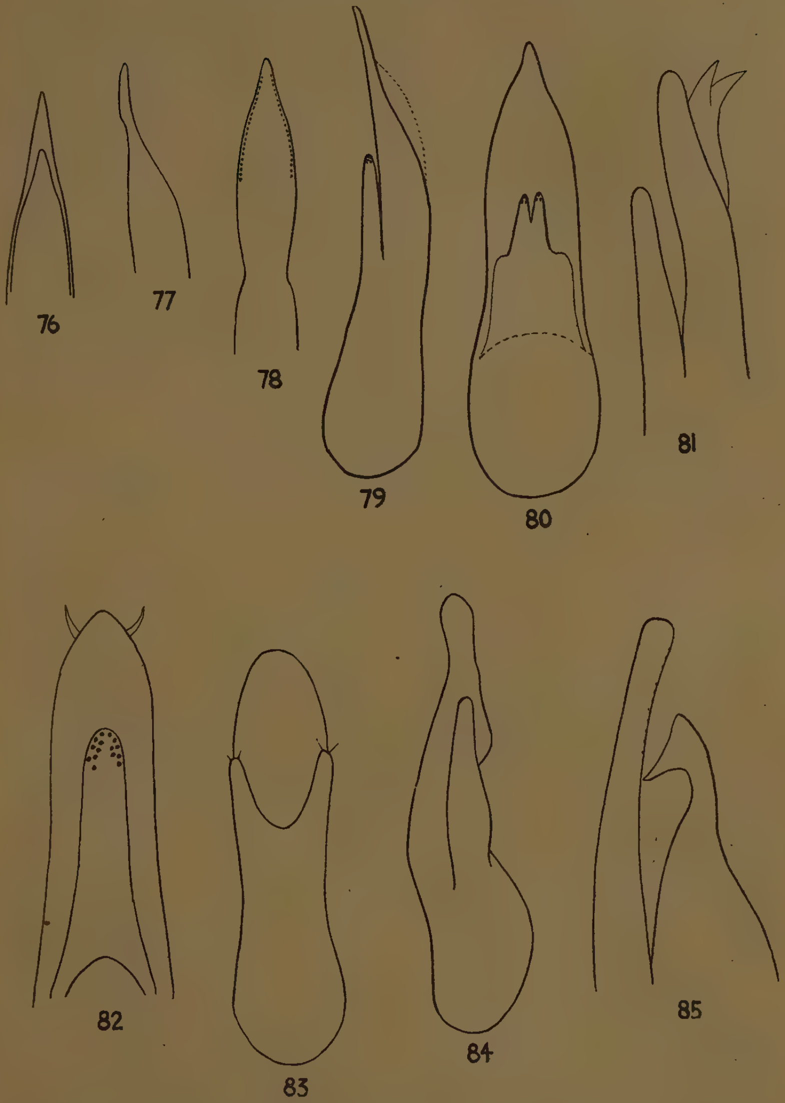
46. *P. robusticornis* Bernhauer.

Bernhauer, 1915, *Ann. Mus. nat. Hung.* **13** : 137.

The aedeagus is shown in figs. 79, 80. The median lobe is very long and slender at the apex when viewed laterally, the paramere is short and narrowed apically, and the apical portion is furcate for about half its length. Each branch of the fork bears a few pegs on the inner face at the extreme apex.

Group 4.—*Discal Series of Thorax Each Consisting of Five Punctures.*

This group contains about 60 African species, including those newly described in this paper. Amongst them are found a number of species which are closely related, difficult to distinguish from one another, and at present in a state of confusion. Firstly there is *P. longicornis* Stephens and its allies. These beetles, which from other characters might well be classed with *P. varians* Paykull and its allies, form a group by themselves because of the peculiar structure of the aedeagus. The paramere is slender and long and is asymmetrically directed towards the right side of the median lobe (viewed from above); it reaches the edge of the median lobe some little distance before the apex. The median lobe is flat, dilated apically and more or less rounded at the apex. Several species have been described from various parts of the African continent, and they differ from one another but slightly, some of the differences being colour of elytra, of legs or of basal segments of the antennae. In view of the fact that the aedeagus differs but little, or not at all, in these species, it may well be that some of them are only colour variations or local races. On the other hand, there is the possibility that in this group the aedeagus fails to be a character by which the species can be separated. It would be necessary to examine



FIGS. 76–85.—(76) *P. parvicornis* Fauvel. Apex of aedeagus, upper view. (77) *P. parvicornis.* Apex of median lobe, lateral view. (78) *P. parvicornis.* Paramere, inner face. (79) *P. robusticornis* Bernhauer. Aedeagus, lateral view. (80) *P. robusticornis.* Aedeagus, upper view. (81) *P. hospes* Erichson. Apex of aedeagus, lateral view. (82) *P. hospes.* Apex of aedeagus, upper view. (83) *P. cupreonitens* Eppelsheim. Aedeagus, upper view. (84) *P. cupreonitens.* Aedeagus, lateral view. (85) *P. meges* sp. n. Apex of aedeagus, lateral view.

a large amount of material from many different localities to be able to clear up the confusion in this group. Secondly, there is the *xanthoraphis-densecaudatus* group. This group, while being in quite as much confusion as the *longicornis* group, will probably be a much simpler one to straighten out if sufficient authenticated specimens could be examined, as the genitalia will probably be of considerable help. The differences between the species are, apart from the genitalia, mainly slight and comparative. As an example of the confusion amongst these species, I have seen three specimens of *P. xanthoraphis* Eppelsheim, one in the Belgian Congo Museum, unfortunately a female, which is quite probably correctly named; two in the British Museum are two other species. One of these, a male, is certainly distinct from the Belgian Congo Museum specimen, but I have been unable to determine to what species it should be referred; the second, also a male, is undoubtedly *P. densecaudatus* Bernhauer, with the type of which I have compared it and its aedeagus; it bears a label in Bernhauer's handwriting, "*P. xanthoraphis* Epp. major ?".

Beyond figuring the aedeagus of a few of the species belonging to these two groups about which I have no doubt, I have omitted them entirely from this paper and from the key which follows.

Even when these species have been omitted, there still remain many species which I have not seen, and consequently the key will be limited in its utility.

Key to the 5-punctate Species.

1. Elytra metallic . . . 2.
   Elytra entirely or in part red, or black marked with red . . . 3.
   Elytra more or less uniformly black or brownish (in a few smaller species brown, lighter towards apex) . . . 8.
2. Head very strongly transverse; thorax transverse; antennae and legs dark . . . 48. *cupreonitens* Eppelsheim.
   Head less transverse; thorax longer than broad; antennae and legs light . . . 47. *hospes* Erichson.
3. Elytra black with a red patch on disc of each . . . *ustus* Fauvel.
   Elytra red, all the margins of each black . . . 4.
   Elytra entirely red (or with suture narrowly black) . . . 5.
   Elytra red with black at basal region . . . 6.
4. Elytra strongly and sparingly punctured; abdominal segments closely and finely punctured at their bases, more sparingly at their apices; antennal segments elongate . . . *ustus* Fauvel v. *ustipennis* Fauvel.
   Elytra more finely, sparingly punctured; antennal segments shorter; size smaller (12 mm.) . . . 49. **meges** sp. n.
5. Elytra entirely red; head transverse; facies of *corruscus* Gravenhorst 50. *ochripennis* Cameron.
   Elytra very narrowly red at suture; head elongate, oval; facies of *varians* Paykull . . . 51. **cumaeus** sp. n.
6. Elytra red, darker round scutellum; antennal segments longer than broad; elytra very finely and closely punctured . 52. *combustus* Fauvel.
   Elytra red, black across the whole basal region . . . 7.
7. Antennae longer; puncturation of elytra closer and finer 53. *sequens* Bernhauer.
   Antennae shorter; puncturation of elytra coarser and less close 54. *caffer* Boheman.

8. Head with posterior angles prominent . . . . . 55. *morio* Boheman.
Head with posterior angles normal . . . . 9.
9. Size larger (10 mm. or more) . . . . 10.
Size smaller (less than 9 mm.) . . . . 11.
Size very small (less than 5 mm.) . . . . 18.
10. Elytra very finely and sparingly punctured; form not narrow and parallel-sided; penultimate segments of antennae not transverse; elytra much wider than thorax . . . . . . 57. *congoensis* Bernhauer.
Elytra moderately strongly, less sparingly punctured; form parallel-sided, narrow, facies of *abyssinus* Fauvel; penultimate segments of antennae longer than broad; elytra only a little wider than thorax 58. **trilobatus** sp. n.
Elytra very closely uniformly punctured; head strongly transverse with marked posterior angles; colour brownish with a crimson tint especially on thorax and elytra . . . . 59. **caedator** sp. n.
11. Elytra testaceous, black around scutellum . . . 65. **marcescens** sp. n.
Elytra brownish, lighter towards base (length 5 mm.) . . . . . 12.
Elytra uniformly black or brownish . . . . 13.
12. Posterior angles of head marked; antennae lighter; suture less markedly lighter; abdomen more strongly and more sparingly punctured . . . . 62. **fraxinatus** sp. n.
Posterior angles of head more rounded; antennae darker; suture more markedly lighter; abdomen more finely and more closely punctured . 63. **sinuatus** sp. n.
13. Head strongly transverse, with anterior margin broadly and markedly concave, with a large depression on vertex . . . 56. **marshalli** sp. n.
Head with normal anterior margin . . . . 14.
14. Penultimate segments of antennae longer than broad . . . . . . 15.
Penultimate segments of antennae not longer than broad . . . . 16.
15. Thorax narrower, parallel-sided; elytra closely and finely punctured *quisquiliarius* Gyllenhal.
Thorax broader, widened behind; elytra more strongly and more sparingly punctured . . . . 64. **lissonurus** sp. n.
16. Scutellum, elytra and abdomen more sparingly punctured; head quadrate; tibiae light, feebly infuscate . . . 60. *dilutipes* Fauvel.
Scutellum, elytra and abdomen more closely punctured . . . . . 17.
17. Head larger, posterior angles more rectangular; antennal segments less transverse; tibiae darker . . . . 61. **sepilibilis** sp. n.
Head smaller, posterior angles more rounded; antennal segments more transverse; tibiae lighter . . . . *ventralis* Gravenhorst.
18. Elytra normally punctured . . . . 19.
Elytra remotely punctured; size very small . . . . 20.
19. Antennae entirely testaceous; elytra longer than broad 67. **tenuissimus** sp. n.
Antennae light only at base and extreme apex; elytra broader than long . . . . 66. *manyemae* Bernhauer.
20. Antennae dark; elytra finely punctured; thorax broader . 68. **turneri** sp. n.
Antennae lighter; elytra more coarsely punctured; thorax narrower *maritimus* Motschulsky.

47. *P. hospes* Erichson.

Erichson, 1843, *Arch. Naturgesch.* 9 (1): 221.

The aedeagus of this species is remarkable for the two horns which may be seen projecting beyond the apex of the median lobe in the upper view. In all the specimens which I have examined these are constant; they appear either to be part of the partially extruded internal sac, or else they are part of the lower face of the median lobe in the region from which the sac is evaginated; it is not possible to tell exactly where they are situated in dried specimens, but they always show in exactly the same place. (Figs. 81, 82.)

48. *P. cupreonitens* Eppelsheim.

Eppelsheim, 1895, *Dtsch. ent. Z.* **1895** : 125.

In this species the paramere is broadly furcate at the apex, the two branches of the fork reaching a little beyond the sides of the median lobe. The median lobe is bent upwards in the apical part from the base of the fork of the paramere, so that it protrudes between the branches. (Figs. 83, 84.)

49. **P. meges** sp. n. ✓

In the short series of *P. ustus* Fauvel in the British Museum there is a specimen bearing a label in Bernhauer's handwriting "*P. ustus* Fvl. var. ?". This specimen is without doubt a different species from the others. In the colour of the elytra it agrees with Fauvel's var. *ustipennis*, but other characters, such as puncturation and the structure of the antennae, are such that it is most unlikely that Fauvel, if he had had this insect before him, would have called it a variety of *ustus*. Assuming that the specimens of *ustus* in the British Museum and also a specimen in my own collection are the true *ustus* Fauvel, the specimen under consideration must be described as new, and I propose for it the name *meges*.

The new species differs from *ustus* Fauvel in the following respects: In build it is more slender; the colour of the whole insect is lighter, the antennae being brown, lighter towards the apex and with the two basal segments much lighter and reddish; the thorax and abdomen are brownish; the elytra are red with a narrow margin of black along the base, lateral margins, apices and suture; the legs are reddish with the tibiae infuscate. The antennal segments are very much longer than in *ustus*, all the segments being considerably longer than broad. The punctures of the head and thorax are a little weaker, the elytra are considerably more finely punctured and the abdomen much more finely punctured than in that species. The tarsi also are a little longer and more slender.

I have not seen the aedeagus of *ustus*; that of *meges* is remarkable both for the form of the paramere and for the shape of the median lobe. The median lobe terminates in a very large, sharply pointed hook; the paramere is deeply divided down the middle into two broad lobes, which are closely studded with pegs. As far as I could judge from the single specimen examined, the lobes do not lie flat, as in fig. 86, but are rather bent round to envelop the sides of the median lobe. (Figs. 85, 86.)

Length: 12 mm.

Type, male, ABYSSINIA: Mt. Zuquála, circa 9000 ft., 22.x.1926 (*Dr. H. Scott*), in the British Museum (Natural History).

50. *P. ochripennis* Cameron.

Cameron, 1929, *Rev. Zool.-Bot. afr.* **18** : 63.

The general form of the aedeagus of this species is similar to that of *cupreonitens* Eppelsheim. It differs, however, in a number of respects in the contours of the median lobe and the paramere, as may be seen from the figures. (Figs. 87, 88.)

51. **P. cumaeus** sp. n.

Size and general build of *P. varians* Paykull, from which it may be distinguished at a glance by the colour of the elytra and by the form of the aedeagus.

Black, with the elytra brownish red, narrowly and obscurely darkened at the suture; base of second segment of the antennae rufous; posterior femora dark brown, nearly black; intermediate and posterior tarsi becoming lighter towards the apex; all the claws pale reddish.

Length: 9 mm.

The new species differs also from *varians* in the following respects; head longer and narrower; scutellum and elytra more sparingly punctured, abdomen also a little more sparingly punctured.

As may be seen from figs. 89, 90, the aedeagus differs considerably from that of *varians* and its allies. Not only is the median lobe much longer and more pointed than in *varians*, but also the paramere is long, slender and acuminate, with pegs at the extreme apex; it lacks the spoon-shaped dilation in the apical portion as seen in *varians*, etc.

Type, unique, male, S. Rhodesia: Mt. Selinda, xi–xii. 1930, in my collection.

52. *P. combustus* Fauvel.

Not only is there a close similarity between this and the two following species in general appearance, but also the aedeagus is of the same general form in all three, but yet with striking distinctions. The paramere is broadly dilated in the apical portion; it is not as broad as the median lobe, in which respect it resembles *sequens* Bernhauer and Schubert, but it is very much broader than in that species. (Figs. 91, 92.)

53. *P. sequens* Bernhauer and Schubert.

Bernhauer and Schubert, 1914, *in* Junk: *Cat. Col.* (*Staph.*) **57**: 355 nom. nov.
= *P. imitator* Fauvel, 1907, *Rev. Ent.* **26**: 44.

The aedeagus resembles that of the previous species, but the median lobe is flatly rounded at the apex instead of being produced as in that species, and the enlarged portion of the paramere is very much smaller and also briefly and narrowly furcate at the apex. (Fig. 93.)

54. *P. caffer* Boheman.

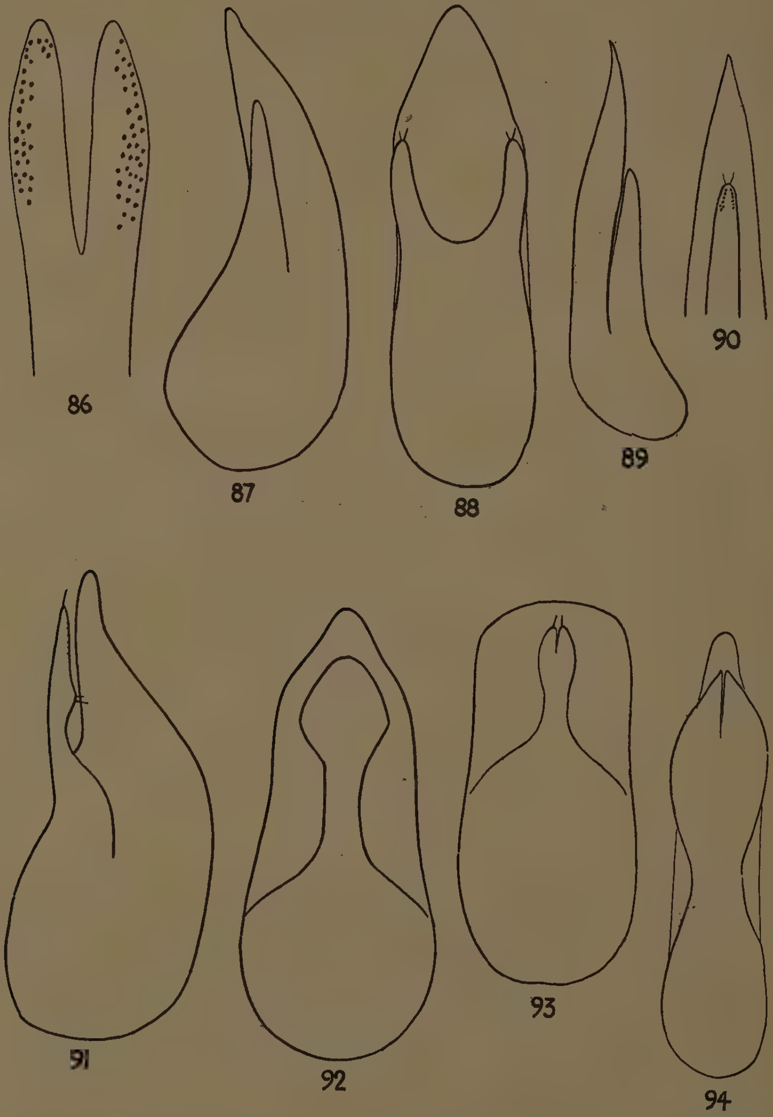
Boheman, 1848, *Ins. Caffr.* **1**: 280.

The aedeagus resembles that of *P. sequens* Bernhauer and Schubert in having a furcate, broadened apical portion to the paramere, but this broadened portion is wider than in that species and than in *P. combustus* Fauvel, and differs from both in being wider than the median lobe. The median lobe is narrow and produced to a rounded point a little beyond the apex of the paramere. In the upper view the greater part of the median lobe is concealed by the paramere (fig. 94). The apex of the paramere on its inner face is studded with numerous pegs, arranged in single rows more or less parallel to the outer margins of the fork, but becoming more scattered and irregular towards the widest part of the paramere. (Fig. 95).

55. *P. morio* Boheman.

Boheman, 1848, *Ins. Caffr.* **1**: 279.

The aedeagus is very long and slender and has a very short paramere. The paramere is narrowly and deeply forked for about half of its length. At the



Figs. 86–94.—(86) *P. meges* sp. n. Apex of paramere, inner face. (87) *P. ochripennis* Cameron. Aedeagus, lateral view. (88) *P. ochripennis*. Aedeagus, upper view. (89) *P. cumaeus* sp. n. Aedeagus, lateral view. (90) *P. cumaeus*. Apex of aedeagus, upper view. (91) *P. combustus* Fauvel. Aedeagus, lateral view. (92) *P. combustus*. Aedeagus, upper view. (93) *P. sequens* Bernhauer. Aedeagus, upper view. (94) *P. caffer* Boheman. Aedeagus, upper view.

extreme apex of each branch there are about 6 pegs arranged in two rows. (Figs. 96–98.)

56. P. **marshalli** sp. n. ✓

Black; head and thorax shining; elytra and abdomen only slightly shining; legs pitchy, femora lighter; antennae with the first segment pitchy brown; palpi pitchy brown.

Head strongly transverse; antennae inserted almost level with the front of the eye; front between the antennae concave; eyes flat; sides behind eyes parallel; longitudinal diameter of the eye as long as the side of the head behind eye; posterior angles broadly rounded, then obliquely straight; base straight; vertex with large triangular depression, whose base extends between the bases of the antennae, and whose apex is between and behind the interocular punctures; interocular punctures twice as distant from one another as from the marginal punctures of the eyes; postocular region finely sprinkled with punctures; two distinct larger punctures behind, on each side, between the eye and the neck, of which the posterior is quite close to the base of the head.

Antennae as long as head and thorax, moderately stout, not thickened towards the apex; third segment a little shorter than the second; fourth to tenth transverse, but not strongly so.

Thorax slightly narrower than the head; sides parallel; much longer than broad; front margin straight; anterior angles rectangularly rounded (viewed from above); posterior angles rounded with the base in a large curve; sides feebly impressed anteriorly; dorsal series each consisting of five moderate punctures, the three middle punctures being closer together than to the outer punctures, arranged much as in *P. rectangulus* Sharp, but the punctures are much finer than in that species; five fine punctures towards the anterior angles; a distinct transverse ground sculpture on both head and thorax.

Scutellum pubescent and punctured, much the same as the elytra.

Elytra much broader than the thorax, about as long as the thorax; broader than long; closely, moderately, fairly deeply and rugosely punctured; pubescence close and fine, short, greyish.

Abdomen very finely and closely punctured, especially at the base of each segment.

Legs moderate, closely pubescent; posterior tarsi as long as the tibiae; first segment longer than the fifth, nearly as long as the three following together.

Length: 8 mm.

Male: The aedeagus is shown in figs. 99, 100.

NATAL: Frere (Marshall coll.), type, unique male, in the British Museum (Natural History).

57. *P. congoensis* Bernhauer.

Bernhauer, 1928, *Wien ent. Ztg.* **45** : 110.

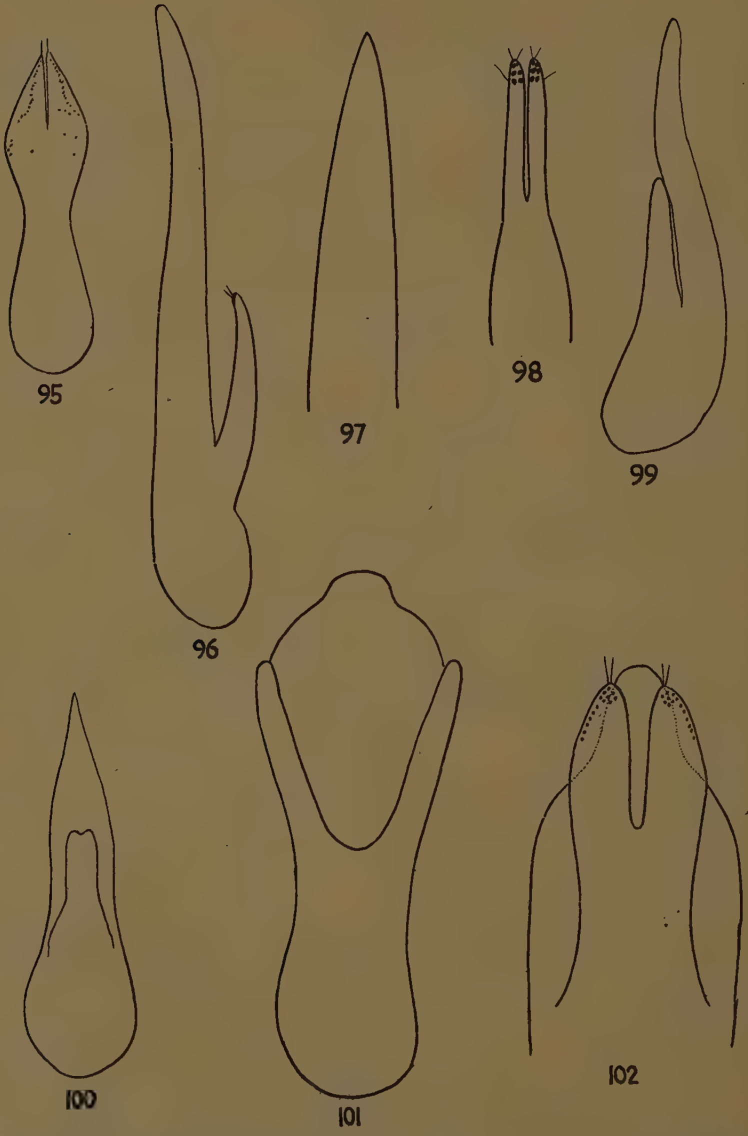
In this species the paramere is broadly and deeply furcate, the branches reaching beyond the sides of the median lobe. The median lobe is broad; at the apex it is rounded, but shortly and broadly produced in the centre (fig. 101). The aedeagus is very similar to that of *purpurcephalicus* sp. n., but differs in the longer fork of the paramere and in the less produced apex of the median lobe.

58. P. **trilobatus** sp. n. ✓

In general appearance something like *P. abyssinus* Fauvel, but easily distinguished from this by the five-punctate discal series of the thorax, as well as by its less transverse head, stout mandibles, much more closely and more finely punctured abdomen, etc.

Elongate, narrow, parallel-sided; entirely black, abdomen with a slight iridescence, legs pitchy, antennae with the base of the second segment clear red.

Head quadrate, scarcely broader than long (male, 20 : 19), flatly rounded in front of the eyes; sides behind eyes parallel, longer than the longitudinal diameter of the eye



Figs. 95–102.—(95) *P. caffer* Boheman. Paramere, inner face. (96) *P. morio* Boheman. Aedeagus, lateral view. (97) *P. morio*. Apex of median lobe, inner face. (98) *P. morio*. Apex of paramere, inner face. (99) *P. marshalli* sp. n. Aedeagus, lateral view. (100) *P. marshalli*. Aedeagus, upper view. (101) *P. congoensis* Bernhauer. Aedeagus, upper view. (102) *P. trilobatus* sp. n. Apex of aedeagus, upper view.

(7 : 5), then obtusely angled and rounded to the neck ; base concave ; eyes flat ; surface smooth and shining ; interocular punctures quite close to and slightly behind the anterior marginal punctures of the eyes, very widely distant from one another ; three other strong punctures along the inner hind margin of each eye ; a strong puncture in the same relative position to the second of these as the interocular puncture bears to the anterior one, on each side ; about twelve other strong punctures on each side in the posterior portion of the head.

Mandibles short, stout, strongly curved, with strong blunt tooth on inner margin.

Antennae as long as head and thorax together, moderately slender, all the segments longer than broad ; first segment stout at apex ; third only slightly longer than second, not much shorter than first ; fourth to sixth increasing in length, distinctly longer than broad ; sixth to tenth decreasing in length ; ninth and tenth only slightly longer than broad ; eleventh about equal to fifth, truncate at apex and slightly acuminate at one side.

Thorax a little wider than head, parallel-sided, a little longer than broad (25 : 22) ; anterior angles obtusely rounded ; anterior margin roundly produced ; posterior angles broadly rounded in even curve with the base. Surface smooth and shining ; dorsal series consisting of five moderate punctures ; the first four of these are evenly spaced, in the type specimen, the fifth is also evenly spaced in the right series, but further apart in the left ; the lateral series consists of four punctures, one near the anterior margin, one level with the third dorsal puncture, two others close together at a level behind the fourth dorsal, obliquely, the fifth dorsal is almost in line with these two ; two others towards the anterior angles between this series and the margin ; marginal punctures all along the base and sides.

Scutellum fairly large, moderately strongly punctured except at base and margins.

Elytra slightly wider than the thorax, at their greatest length as long as together broad ; moderately strongly and sparsely punctured ; pubescence moderate, dark.

Abdomen much more closely punctured than the elytra, punctures finer than on the elytra ; those on the basal segments as strong as on the scutellum ; the punctures becoming very fine on the apical segments.

Legs short ; tibiae moderately spinose ; anterior tarsi strongly dilated in male ; intermediate and posterior tarsi about as long as the tibiae, with first segment slightly longer than fifth, equal to the second and third together.

Underside ; head with an oblique row of obsolete punctures from the base of the mandibles to the centre of the head near the base ; there is a distinct but shallow depression in the middle of this row ; metasternum distinctly, finely and sparsely punctured ; abdomen punctured as above.

Male : Eighth sternite broadly, triangularly excised in the apical margin. The aedeagus is short ; the median lobe is broad, strongly narrowed at the apex, where it is broadly rounded ; the paramere is nearly as long as the median lobe, deeply and narrowly furcate (figs. 102, 103).

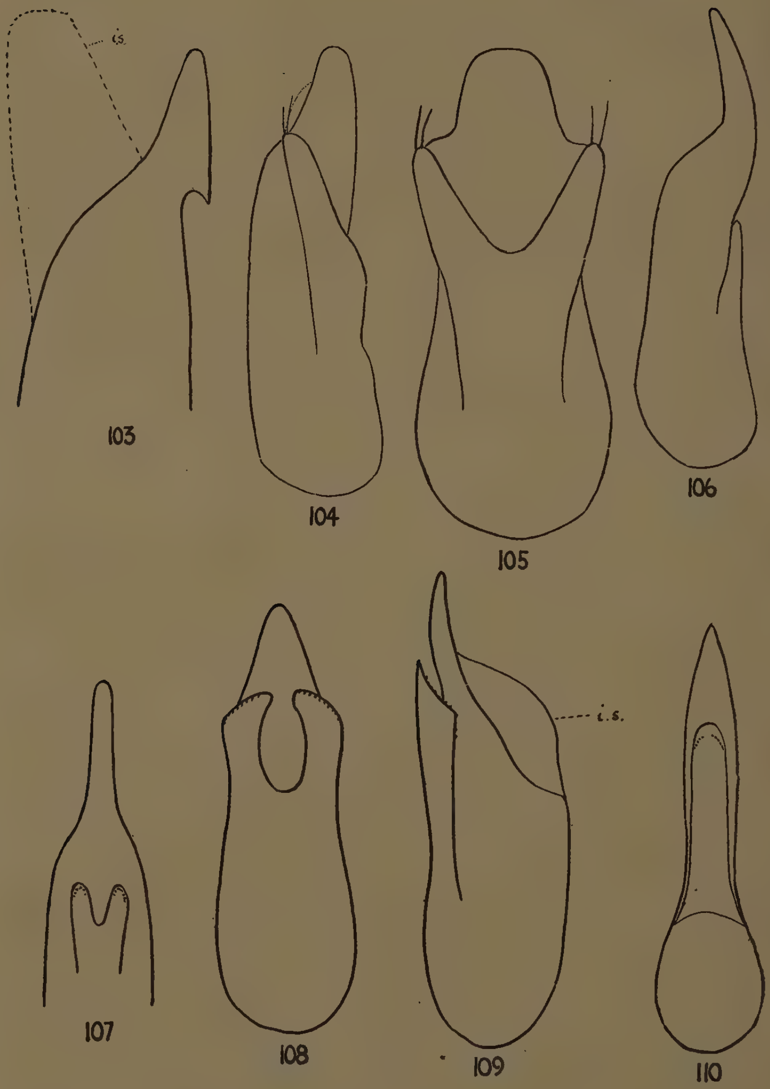
Length : 12 mm.

Type, male, unique, Lubero, 23/24.viii.1932 (*L. Burgeon*), in the Musée du Congo Belge.

59. **P. caedator** sp. n.

Head and thorax iridescent purple and green ; elytra and abdomen pitchy ; antennae black with the apical segment reddish brown ; mouth parts and legs brownish.

Head (male) strongly transverse (14 : 11), very little produced in front of eyes, front straight ; sides straight, very slightly convergent behind eyes ; longitudinal diameter of eye about twice as long as sides behind eye ; posterior angles very obtuse and rounded ; base straight. Interocular punctures near the anterior marginal punctures of the eyes, but a little anterior to them, considerably distant from one another, almost as far apart as the bases of the antennae ; three punctures along the inner hind margin of the eye ; another, on each side, level with the first of these, behind the interocular puncture ; a few more punctures near the base at each side of the head.



FIGS. 103–110.—(103) *P. trilobatus* sp. n. Apex of median lobe, lateral view. (104) *P. caedator* sp. n. Aedeagus, lateral view. (105) *P. caedator*. Aedeagus, upper view. (106) *P. dilutipes* Fauvel. Aedeagus, lateral view. (107) *P. dilutipes*. Apex of aedeagus, upper view. (108) *P. sepilibilis* sp. n. Aedeagus, upper view. (109) *P. sepilibilis*. Aedeagus, lateral view. (110) *P. sinuatus* sp. n. Aedeagus, upper view.

Mandibles long and slender, feebly toothed on inner margin.

Antennae short and rather stout; third segment a little longer than the second, much shorter than the first; fourth to tenth slightly decreasing in length, fourth slightly transverse, tenth distinctly transverse; eleventh on its longer side twice the length of the tenth.

Thorax at anterior angles as wide as head, as wide as long; anterior angles, viewed from above, almost rectangular; sides straight and divergent for anterior half, strongly rounded in middle, slightly rounded behind; posterior angles marked, very obtuse; base rounded in a large curve. Dorsal series each consisting of five punctures, in a slightly arcuate row, the first four equidistant, the fifth a little more distant; three lateral punctures make a straight line with the fifth discal to the anterior angle; two others and the fourth discal make another line parallel with this; marginal punctures minute and obsolete.

Scutellum as broad as long, finely punctured throughout as on the elytra.

Elytra wider than thorax (9·5 : 7·2), widened behind, together wider at apex than their greatest length (9·5 : 8); very closely, evenly and finely punctured, with three longitudinal rows, one close to suture, and two on disc, of four small setiferous punctures.

Abdominal puncturation on basal segments similar to that of elytra, but very much finer towards the apex.

Tibiae moderately spinose; posterior tarsi distinctly shorter than the tibiae, with the first segment a little longer than the fifth, about equal to the second and third together.

Underside; head smooth; intermediate coxae widely distant; metasternum punctured as base of abdomen; abdomen punctured as above.

Length: 10 mm.

Male: Anterior tarsi simple; eighth sternite with its apical margin broadly and shallowly emarginate. The aedeagus is very distinct; the apex of the median lobe is almost truncate, feebly rounded, and very broad; the paramere is widely furcate, the two branches enveloping the sides of the median lobe (figs. 104, 105).

HAUTE-UELE: Watsa, xi.1919 (*L. Burgeon*). Type, unique male, in the Musée du Congo Belge.

60. *P. dilutipes* Fauvel.

Fauvel, 1898, *Rev. Ent.* **17**: 117.

The aedeagus is distinct by reason of its very long, bent, produced apical portion of the median lobe and its small forked paramere. In both these respects it resembles that of *P. ventralis* Gravenhorst; in fact the aedeagus differs but little in the two species, but, as will be seen from the figure, the fork of the paramere is a little different from that of *ventralis*. (Figs. 106, 107.)

61. **P. sepilibilis** sp. n. ✓

Pitchy black, abdomen with slight iridescence, antennae dark with basal segment lighter, mouth parts pitchy brown, legs pitchy with yellowish brown femora. In some specimens the legs and antennae are much lighter than in the type.

Head transverse in both sexes, but much larger and more rectangular in the male than in the female; slightly produced in front of the eyes, with the front straight; sides parallel; hind angles rectangular but rounded; posterior margin nearly straight, slightly concave. There is a large, deep, long-oval depression on the vertex in front. Eyes moderate, their longitudinal diameter being about equal to the length of the lateral margins of the head behind eyes. Anterior ocular punctures situated before the middle of the inner margin of the eyes; interocular punctures almost in a straight line with these, and near to them, widely separated from one another; two other punctures close to each eye, one at the inner posterior angle and the other behind the eye; one other puncture, on each side, behind the former of these two, but nearer the middle of the head, and another at the extreme base of the head ; several small marginal punctures in the posterior angles of the head ; head covered with a distinct ground sculpture.

Mandibles long and slender, strongly curved at apex, finely and acutely toothed in the middle of the inner margin.

Antennae with the second and third segments subequal, fourth to seventh decreasing in length, but slightly longer than broad, eighth to tenth quadrate, eleventh short about equal to sixth.

Thorax a little narrower than the head in the male, as wide as the head in the female ; sides parallel ; anterior angles strongly depressed, widely rectangularly rounded if viewed from the side, if viewed from above evenly rounded with the anterior margin, which is slightly convex ; posterior angles rounded with the base. Discal series each consisting of five strong punctures, the three in the middle being closer to one another than to the first and fifth, but not so obviously as in such species as *P. rectangulus* Sharp. On each side there is a lateral series of three punctures, the anterior one of which is close to the anterior margin ; this series is parallel to the discal series ; in addition there are a few small marginal punctures. Ground sculpture as on the head.

Scutellum closely and fairly strongly punctured and pubescent.

Elytra wider than the thorax, slightly shorter than the thorax at the suture, but longer at the sides ; puncturation fairly strong and close ; pubescence long, yellowish grey.

Abdomen very finely punctured, less towards the middle of the anterior segments and towards the apex of the abdomen, more at the sides of the front segment.

Legs short ; posterior tarsi with first segment equal to fifth, and much shorter than the second, third and fourth together.

Length : 6–7 mm.

Male : Anterior tarsi scarcely dilated ; eighth sternite with a very small triangular excision in the apical margin, the emargination almost entirely filled with membrane. The structure of the aedeagus is shown in figs. 108, 109 ; it will be seen to differ markedly from that of *ventralis* Gravenhorst.

Congo region, without further data ; type male in my collection. I have subsequently seen specimens of the same species from Mongende, 21.iv.1921 (*Dr. H. Schouteden*) ; Leopoldville, 1930 (*A. Tinant*) ; Equateur, Bokote (*R. P. Hulstaert*) ; Haut Uele : Watsa, xi–1919 (*L. Burgeon*) : all in the Musée du Congo Belge.

This species comes very close to *P. ventralis* Gravenhorst and the specimens which I have seen from the Belgian Congo Museum were so determined by Bernhauer. It may be distinguished from that species by the shape of the head which is more transverse and rectangular. In the male the head is much larger and wider than in *ventralis* and the posterior angles are rectangular but rounded. In the female the head is less rectangular in shape than in the male, but the sides behind the eyes are not narrowed as in *ventralis*, and the posterior angles are more prominent. In both sexes the eyes are larger than in *ventralis* and consequently the length of the sides of the head behind the eyes is less. In the male there is a large deep depression in the centre of the head in front ; this is much smaller and less distinct in the female. This depression in the male almost approaches that of *rectangulus* Sharp, and at first sight the head appears rather similar to that of that species, but the hind angles are quite different, being rounded in *sepilibilis*. The antennal segments in *sepilibilis* are a little longer than in *ventralis*, the fourth to sixth being distinctly longer than broad, and the penultimate segments quadrate, or scarcely transverse. The most obvious distinction, however, lies in the aedeagus, as may be seen from the accompanying figures.

62. **P. fraxinatus** sp. n.

A small species apparently related to *P. ventralis* Gravenhorst.

Head black; thorax pitchy brown; elytra a little lighter than the thorax, pitchy brown towards the base and on the disc, becoming lighter and more reddish brown apically; abdomen dark pitchy brown with the hind margins of the segments brown, much lighter; palpi dark brown; legs and antennae reddish brown.

Head rather quadrate, broader than long (9 : 8), considerably produced and rounded in front; sides together with the ocular margins a little rounded; eyes longer than the sides behind eyes (3 : 2); posterior angles marked, not very obtuse; base straight; interocular punctures very widely distant from one another, and very close to the marginal punctures of the eyes; ground sculpture very strong, more or less transverse.

Antennae very short, a little thickened towards apex; third segment a little shorter than second, and rather shorter than usual; fourth to tenth very transverse; eleventh very short.

Thorax as wide as the head, about as long as wide, cylindrical; anterior margin rounded; anterior angles obtusely rounded; sides straight, parallel; posterior angles and base very obtusely rounded; dorsal series each consisting of five strong, more or less equidistant punctures; usual lateral punctures; ground sculpture as on the head.

Scutellum finely punctured.

Elytra a little broader than the thorax (5·2 : 4·2), a little broader than long (5·2 : 5), shining, moderately and fairly closely punctured.

Abdomen a little dull, as closely punctured as the elytra, but a little more finely.

Posterior tarsi as long as the tibiae, first segment as long as the fifth, and as long as the second and third together.

Length: 5 mm.

Upper Senegal: Badoumbe, 1.v.1882 (*Dr. Nodier*), type, unique female, in the Musée du Congo Belge.

63. **P. sinuatus** sp. n. ✓

This species is so closely related to *P. fraxinatus* sp. n. as to need no separate description; it will suffice to point out the differences. *P. sinuatus* may be distinguished from that species by the rounded posterior angles of the head, by its darker antennae, by its longer elytra, which have a more markedly pale suture, by the closer and finer puncturation of the elytra, and by the finer and much closer puncturation of the abdomen, especially on the apical segments. The aedeagus is shown in figs. 110, 111. The oblique arrangement of the pegs is peculiar.

N.W. Rhodesia: Kashitu, N. of Broken Hill, 26.iii.1915 (*H. C. Dollman*), type, unique male, in the British Museum (Natural History).

P. sinuatus and *P. fraxinatus* both bear some resemblance to *P. kashituensis* mihi, but may be separated at once by the 4-punctate thorax and the much more transverse antennal segments of that species. Although superficially *P. sinuatus* appears to be related to *P. ventralis* Gravenhorst, the structure of the aedeagus would separate it from this species and its allies.

64. **P. lissonurus** sp. n. ✓

Black; head and thorax shining; elytra with a distinct brownish colour; abdomen rather iridescent; mouth parts pitchy; antennae blackish with the first and extreme base of the second segments reddish; legs yellowish brown with tibiae infuscate.

Head slightly transverse, oval; rounded in front of the eyes; eyes a little prominent; sides behind eyes convergent and rounded with the posterior angles of the head; base wide, straight; eyes large, their longitudinal diameter much longer (18 : 7) than the lateral margins of the head behind eyes; interocular punctures anterior to the marginal punctures of the eyes, the distance between them being more than twice their distance from the marginal punctures (6 : 16 : 6); a few small punctures in the postocular region.

Antennae much longer than the head and thorax; all the segments distinctly longer than broad.

Thorax wider than the head, truncate in front, longer than broad (5·5 : 5), wider behind than in front (5·5 : 4); anterior angles very obtusely rounded; sides straight, divergent posteriorly, but with a small distinct concavity in the middle; posterior angles broadly rounded with the broad base; discal series widely separated, each consisting of five moderate punctures, of which the first four are more or less equidistant, but the fifth is more remote, as distant from the fourth as from the base; usual lateral punctures.

Scutellum large, closely and finely punctured.

Elytra broader than the thorax and about as long, broader than long (7 : 5·5); puncturation close, fine, asperate; pubescence coarse and thick.

Abdomen rather finely and rather diffusely punctured.

Posterior tarsi with the first segment a little longer than the fifth, about equal to the second and third together.

Length: 5 mm.

Male: Anterior tarsi broadly dilated; the aedeagus is shown in figs. 112, 113.

EQUATEUR: Boende, 1928 (*R. P. Hulstaert*), type, unique male, in the Musée du Congo Belge.

This species is of the *longicornis* Stephens facies, but much smaller; the dark brown elytra with their coarse pubescence, which makes a distinct fringe at the sides, the rather broad head, rather sparingly punctured abdomen and the structure of the aedeagus will serve to distinguish the species.

65. **P. marcescens** sp. n.

Pitchy brown; elytra testaceous, black around scutellum and suture; elytra and abdomen densely clothed with long yellowish pubescence; palpi brown; legs and antennae testaceous.

Head round, wider than long; broadly rounded in front; eyes large, their longitudinal diameter three times as long as the sides of the head behind eyes measured to the bristle; posterior angles broadly rounded; base broadly concave; microsculpture strong, transverse, composed of nearly straight lines, especially on basal half; interocular punctures very small, situated near the marginal punctures of the eyes; a few other distinct punctures in the postocular region.

Antennae as long as head and thorax together, rather stout; second segment equal to the third; fourth and fifth quadrate; sixth to tenth transverse, but not strongly so.

Thorax as long as broad, strongly widened behind; anterior margin truncate; anterior angles marked, obtuse; sides rounded, diverging posteriorly; posterior angles broadly rounded with base; discal series each consisting of five moderately small, close punctures; ground sculpture as on the head.

Scutellum large, long, closely punctured and with long, close, yellow pubescence.

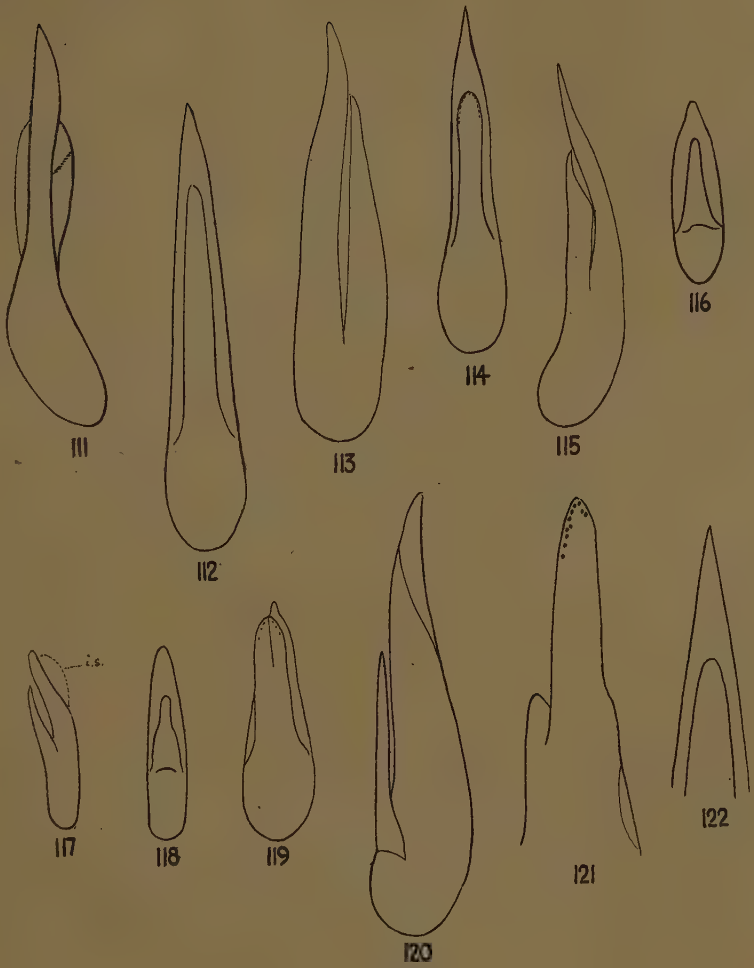
Elytra closely and finely punctured, as the scutellum, and with long pale pubescence; broader than long; widened behind.

Abdomen more closely and more finely punctured than the elytra, but with similar pubescence.

Length: 6 mm.

Male: The aedeagus is shown in figs. 114, 115.

JEBEL HAINA, (*R. C. Darling*), 27.i.1930, dung, Sudan Govt., type, male, in the British Museum (Natural History).



Figs. 111–122.—(111) *P. sinuatus* sp. n. Aedeagus, lateral view. (112) *P. lissonurus* sp. n. Aedeagus, upper view. (113) *P. lissonurus*. Aedeagus, lateral view. (114) *P. marcescens* sp. n. Aedeagus, upper view. (115) *P. marcescens*. Aedeagus, lateral view. (116) *P. manyemae* Bernhauer. Aedeagus, upper view. (117) *P. manyemae*. Aedeagus, lateral view. (118) *P. tenuissimus* sp. n. Aedeagus, upper view. (119) *P. turneri* sp. n. Aedeagus, upper view. (120) *P. densecaudatus* Bernhauer. Aedeagus, lateral view. (121) *P. densecaudatus*. Apex of paramere, inner face. (122) *P. densecaudatus*. Apex of aedeagus, upper view.

66. *P. manyemae* Bernhauer.

Bernhauer, 1932, *Rev. Zool.-Bot. afr.* **22** : 148.

The aedeagus is shown in figs. 116, 117, and is of typical *Philonthus* form. I do not think that this species should be included in *Gabrius*, in which subgenus Bernhauer placed it.

67. **P. tenuissimus** sp. n. ✓

Pitchy black; mouth parts, antennae and legs brownish testaceous.

Head rectangular, longer than broad, front straight; sides parallel; posterior angles obtusely rounded; eyes flat, very small, half the length of the sides behind (measured to the bristle); interocular punctures very close to the marginal punctures of the eyes, widely separated from one another; a pair of distinct punctures about the middle of the head, making a rectangle with the interocular pair; another pair towards the neck, a little closer to one another; postocular region smooth.

Antennae shorter than the head and thorax together; second segment equal to the third; fourth as long as broad, fifth to tenth transverse.

Thorax in front as wide as the head, wider behind; anterior margin broadly convex, anterior angles very obtusely rounded; sides almost straight, feebly diverging posteriorly; posterior angles very broadly rounded with the base; thorax longer than broad (2·7 : 2·1); discal series each consisting of five not strong, equidisant punctures, the distance between the fourth and fifth being less than the distance of the fifth from the base; usual lateral punctures; ground sculpture, as on the head, not visible.

Scutellum with a few small moderate punctures.

Elytra as long as together broad, longer than the thorax, widened behind; puncturation rather strong, not deep, not close; pubescence very scanty, yellowish.

Abdomen very finely and diffusely punctured.

Posterior tarsi with the first segment equal to the fifth, less than the second and third together.

Length: 3 mm.

Male: The form of the aedeagus is shown in fig. 118.

NATAL: Kloof, 1500 ft., viii.1926 (*R. E. Turner*). Type in British Museum (Natural History).

68. **P. turneri** sp. n. ✓

Black; legs brown; antennae pitchy, lighter at base.

Head quadrate, longer than broad (3 : 2·5); sides nearly parallel; feebly widened behind; front broadly convex, rounded; posterior angles very broadly and obtusely rounded; longitudinal diameter of the eyes less than the length of the sides of the head behind eyes measured to bristle (9 : 12); interocular punctures very close to the marginal punctures of the eyes, widely separated from one another; another pair of punctures about the middle of the head as widely distant from one another; a third pair towards the neck, a little closer to one another; postocular region impunctate except for a few marginal punctures.

Antennae shorter than the head and thorax together; third segment longer than the second; fourth quadrate; the remainder slightly decreasing in length, feebly transverse.

Thorax a little wider than the head, longer than broad; sides parallel; anterior angles rounded, a little obtuse; posterior angles broadly rounded with the base; discal series each consisting of five punctures; the third of these is closer to the fourth and out of line; the fifth is equidistant from the fourth and the base. Ground sculpture, as also on the head, large, widely spaced, not deep, very irregular.

Scutellum with a few large shallow punctures.

Elytra longer than broad, as long as the thorax; rather strongly, rather sparingly punctured; pubescence scanty, yellowish.

Abdomen much more finely and closely punctured than the elytra, more on the third and fourth (visible) segments than on the others.

Posterior tarsi with the first segment equal to the fifth and shorter than the second and third together.

Length : 4·5 mm.

Male : The aedeagus is shown in fig. 119.

NATAL : Van Reengen, Drakensberg, 1–22.i.1927 (*R. E. Turner*). Type, male, in the British Museum (Natural History).

69. *P. densecaudatus* Bernhauer.

Bernhauer, 1928, *Wien ent. Ztg.* **45** : 109.

The aedeagus has been figured from the type specimen. It is in the main of typical form, but in one respect calls for comment. There is a very distinct shoulder near the base of the paramere on one side only. This is suggestive of a forked paramere in which one branch has in the course of evolution become lost. This shoulder is also reminiscent of the much less marked shoulder, on the same side, in the asymmetrically placed parameres of the species of the *longicornis* group. (Figs. 120–122.)

70. *P. circumcinctus* Eppelsheim.

Eppelsheim, 1895, *Ann. Mus. stor. nat. Genova* **35** : 204.

The aedeagus has been figured from a specimen determined as this species in the British Museum. It very closely resembles that of *P. densecaudatus* Bernhauer, but lacks the marked shoulder at the base of the paramere. (Figs. 123, 124.)

71. *P. minutus* Boheman.

Boheman, 1848, *Ins. Caffr.* **1** : 279.

The aedeagus is very similar to that of *P. agilis* Gravenhorst, but the paramere is shorter. (Fig. 125.)

72. *P. bisignatus* Boheman.

Boheman, 1848, *Ins. Caffr.* **1** : 282.

The aedeagus of this species scarcely differs from that of *P. longicornis* Stephens. (Fig. 126.)

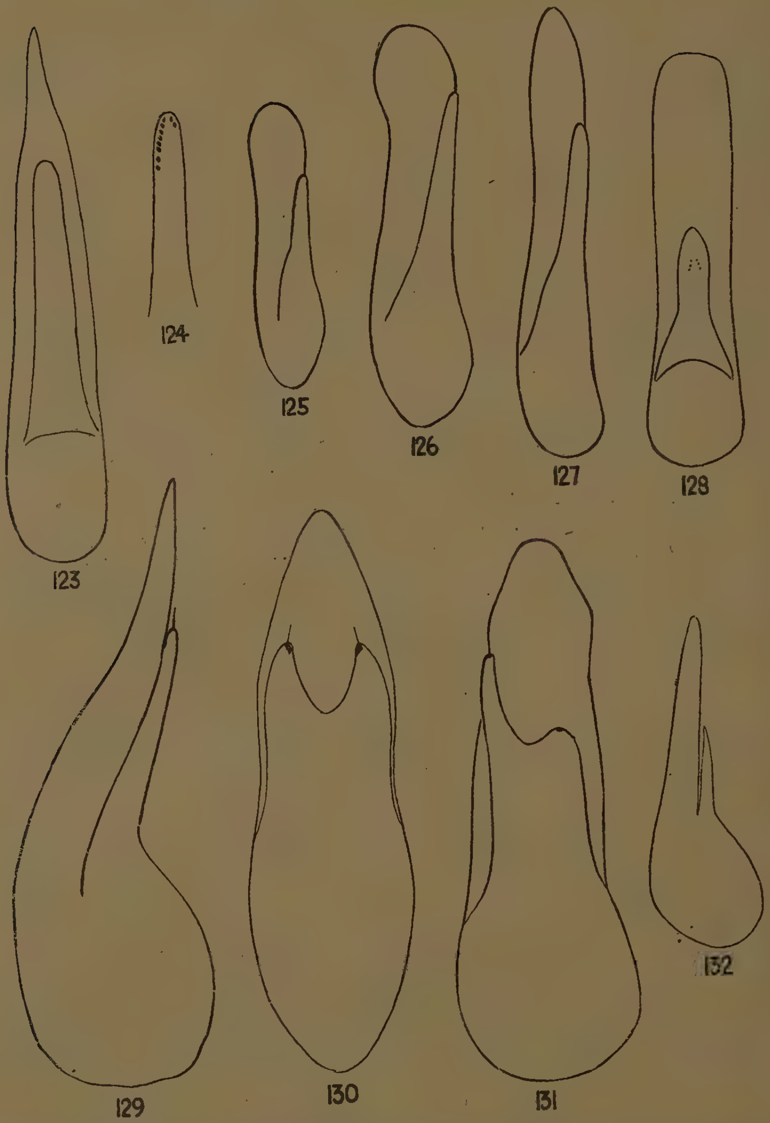
73. *P. peregrinus* Fauvel.

Fauvel, 1866, *Ann. Soc. ent. Fr.* (4) **6** : 315.

Whereas the aedeagus of this species is of the same form as that of other species of the *longicornis* group, it differs distinctly from them in the narrower median lobe which has a much less rounded apex, in fact it is slightly pointed. (Fig. 127.)

Group 5.—*Discal Series of Thoracic Punctures Each Consisting of Six Punctures.*

Having seen less than half of the species belonging to this group in Africa I am not attempting to give a key. Six new species are here described, and the aedeagus of 15 species is here figured.



Figs. 123–132.—(123) *P. circumcinctus* Eppelsheim. Aedeagus, upper view. (124) *P. circumcinctus*. Apex of paramere, inner face. (125) *P. minutus* Boheman. Aedeagus, upper view. (126) *P. bisignatus* Boheman. Aedeagus, upper view. (127) *P. peregrinus* Fauvel. Aedeagus, upper view. (128) *P. constricticeps* sp. n. Aedeagus, upper view. (129) *P. mocquerysi* Fauvel. Aedeagus, lateral view. (130) *P. mocquerysi* Aedeagus, upper view. (131) *P. sanguineus* Fauvel. Aedeagus, upper view. (132) *P. kraatzi* Bernhauer. Aedeagus, lateral view.

74. **P. constricticeps** sp. n. ✓

A species of the facies of *P. longicornis* Stephens, but with red elytra and with the discal series of thoracic punctures each consisting of six punctures.

Head, thorax and scutellum black ; elytra red, with suture narrowly black, and reflexed margins infuscate ; abdomen black with a strong green metallic reflection ; antennae pitchy brown, with the first segment testaceous ; legs yellow testaceous.

Head oval, a little longer than broad ; front straight ; eyes nearly as long as the sides of the head behind eyes ; interocular punctures widely distant from one another, three times as distant as from the marginal punctures of the eyes, and a little anterior to them ; a few punctures at the inner hind angles of the eyes and in the postocular region.

Antennae moderately long ; third segment a little longer than the second, not much shorter than the first ; fourth to tenth increasing in width, decreasing in length ; fourth much longer than broad, seventh quadrate ; eighth to tenth transverse ; eleventh short, less than the two preceding together.

Thorax much broader than the head, very strongly narrowed anteriorly ; anterior margin truncate ; anterior angles rounded ; sides nearly straight ; posterior angles forming a large continuous curve with the base ; thorax as broad as long ; discal series each consisting of six fine punctures ; usual lateral punctures.

Elytra a little wider than the thorax, a little widened behind, a little broader than long ; closely, moderately finely punctured ; pubescence long and light.

Abdomen at base punctured much as the elytra, but more sparingly towards the hind margins of the middle segments, and very sparingly towards the apex.

Posterior tarsi with the first segment distinctly longer than the fifth, equal to the three following together.

Length : 9·5 mm.

MASHONALAND : Salisbury (Marshall coll.), type and eight others in the British Museum (Natural History).

The aedeagus, fig. 128, has a long, broad, parallel-sided median lobe, with the apex feebly curved, nearly truncate. The paramere is short, a little widened in the apical half, and has six pegs in the centre of the widened portion.

75. *P. mocquerysi* Fauvel.

Fauvel, 1903, *Ark. Zool.* **1** : 241.

The aedeagus, which appears typical in the lateral view, is, however, remarkable for the unusual form of the furcation of the paramere as may be seen from the figure. There appear to be very few pegs, situated at the extreme apex. (Figs. 129, 130.)

76. *P. sanguineus* Fauvel.

Fauvel, 1907, *Rev. Ent.* **26** : 46.

The aedeagus is remarkable for its asymmetrical paramere, In this respect it resembles *P. bicoloripennis* Bernhauer, except for the fact that the asymmetry is on the opposite side. (Fig. 131.)

77. *P. kraatzi* Bernhauer.

Bernhauer, 1908, *Denkschr. med.-naturw. Ges. Jena* **13** : 110.

This species has a very curious paramere, which is slightly widened at the extreme apex, with a broad apical margin which is shallowly concave, and with the apical angles obliquely truncate. Apparently there are no pegs. (Figs. 132, 133.)

78. *P. maculipennis* Fauvel.

Fauvel, 1903, *Ark. Zool.* 1 : 242.

The aedeagus has a long parallel-sided median lobe with a feebly rounded, almost truncate apex. The paramere is exceptionally small and furcate. (Fig. 134.)

79. **P. smaragdinus** sp. n. √

Head black, with distinct iridescence ; thorax black with a strong purple iridescence ; elytra dull pitchy black ; abdomen strongly iridescent, green or purple according to the angle from which it is viewed ; antennae pitchy brown, basal segment a little lighter ; legs dirty reddish brown, femora lighter.

Head almost round, about as long as broad ; front feebly rounded ; eyes moderate, their longitudinal diameter about as long as the lateral margin of the head behind eye measured to the neck ; the bristle of the posterior angle is close to the eye ; sides behind eyes nearly parallel as far as the bristle, then strongly rounded to the neck ; base concave ; surface covered with a faint, more or less transverse ground sculpture with a few minute scattered punctures ; interocular punctures twice as distant from one another as from the marginal punctures of the eyes ; postocular region with a few small punctures, bordered interiorly with several stronger punctures.

Antennae with the second and third segments about equal, not very much shorter than the first ; fifth and sixth about equal in length, twice as long as broad ; fourth much longer than broad, but not as long as the fifth ; seventh and eighth about equal to the fourth ; ninth shorter, but longer than broad ; the rest missing in the unique type.

Thorax broader than the head ; anterior margin truncate ; sides feebly rounded, divergent behind ; posterior angles obtusely rounded ; base broadly rounded ; thorax longer than broad ; base wider than the anterior margin ; surface covered with a close, fine microsculpture of oblique lines (forward and outward) ; discal series each consisting of six moderate punctures, which are equidistant except for the sixth, which is a little nearer to the fifth ; lateral series of three punctures in a curve and two in the anterior angles parallel to the sides.

Scutellum closely and finely punctured.

Elytra at base as wide as the thorax, slightly wider behind, a little broader together than long ; closely, finely, asperately punctured and densely pubescent ; pubescence grey.

Abdomen punctured about as strongly as the elytra at the base, but considerably more sparingly ; the puncturation becomes finer and more sparing towards the apex.

Legs moderate ; posterior tarsi as long as the tibiae ; first segment of posterior tarsi much longer than the fifth, a little longer than the second and third together. All the coxae dark.

Length : 9 mm.

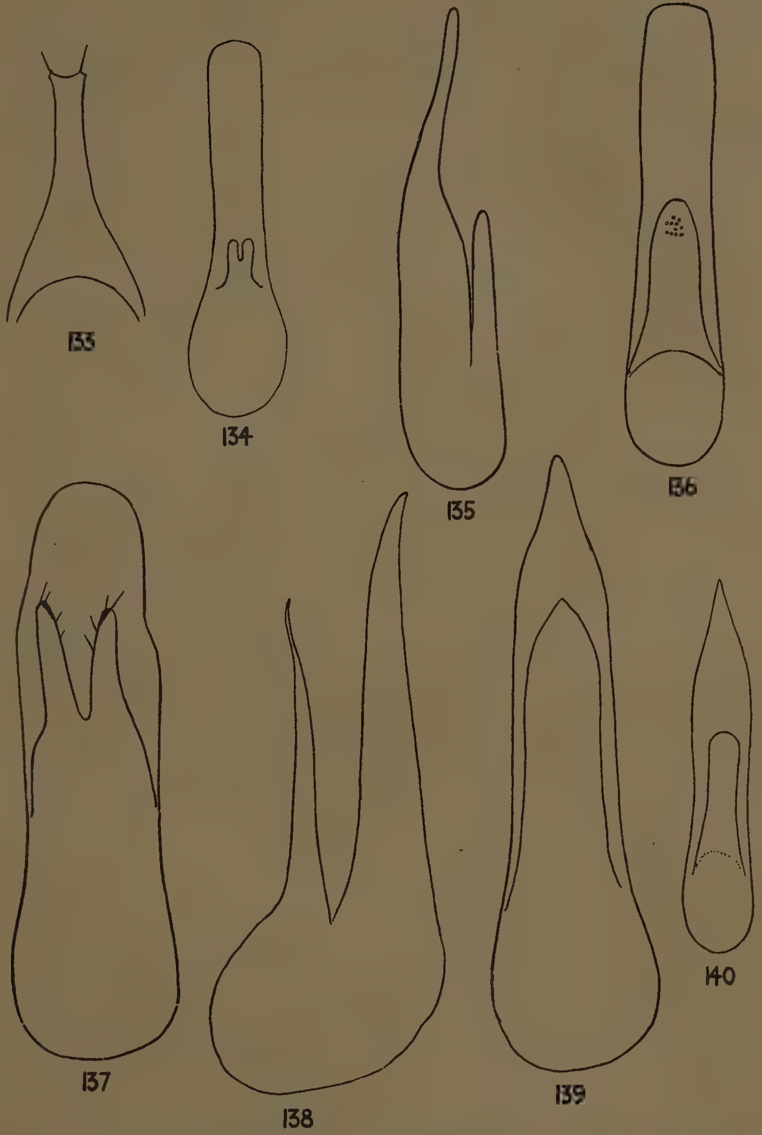
Male : Anterior tarsi a little dilated ; eighth sternite with a small triangular emargination in its apical margin ; the aedeagus is remarkable for its very short paramere and its very broad almost square apex of the median lobe. (*See* figs. 135, 136.)

ITURI : Blukwa, 3.xi.1929 (*A. Collart*), type, unique male, in the Musée du Congo Belge.

80. **P. rhodesianus** sp. n. √

Head and thorax black ; elytra and abdomen pitchy ; legs yellowish brown, femora lighter ; palpi yellowish brown ; antennae with three basal segments brown, the rest dark brown ; abdominal segments with the extreme apical margins brown.

Head slightly transverse, considerably produced in front of the eyes ; front narrow, produced, slightly concave ; sides behind eyes distinctly converging ; posterior angles



Figs. 133–140. (133) *P. kraatzi* Bernhauer. Paramere, inner face. (134) *P. maculipennis* Fauvel. Aedeagus, upper view. (135) *P. smaragdinus* sp. n. Aedeagus, lateral view. (136) *P. smaragdinus.* Aedeagus, upper view. (137) *P. rhodesianus* sp. n. Aedeagus, upper view. (138) *P. aethiopicus* Bernhauer. Aedeagus, lateral view. (139) *P. aethiopicus.* Aedeagus, upper view. (140) *P. rapaciosus* sp. n. Aedeagus, upper view.

broadly rounded; base straight; head widest towards the front of the eyes; eyes prominent, large, occupying more than two-thirds of the sides of the head. There are two transverse oval depressions between the bases of the antennae. Interocular punctures large, a little closer to one another than to the marginal punctures of the eyes; a few moderate punctures along the inner margins of the eyes and in the postocular region, and two large punctures bordering the latter on the inside.

Antennae longer than the head and thorax together; second segment equal to the third, a little shorter than the first; fourth longer than broad; fifth quadrate; sixth to tenth decreasing in length, transverse, sixth slightly, tenth strongly, so; all the segments slightly thickened apically.

Thorax as long as broad; front straight; anterior angles almost rectangular, viewed from above; sides straight, distinctly convergent anteriorly; posterior angles rounded with the base in a large curve. Discal series each consisting of six fairly large, but not deep, punctures; lateral series of three widely spaced small punctures, and two other punctures across the anterior angle.

Scutellum moderately punctured.

Elytra shining, moderately and rather diffusely punctured; longer than the thorax, and longer than together broad.

Abdomen with the puncturation fine and fairly close at the bases of the segments, sparse at the apices; puncturation finer towards the apical segments.

Legs slender; tibial spurs long, black, distinct; posterior tarsi about equal to the tibiae, with the first segment longer than the fifth, about equal to the three following together.

Length 13 mm.

Male: Anterior tarsi with the first three segments broadly, the fourth slightly, dilated; the aedeagus is shown in fig. 137.

N.W. Rhodesia: Kashitu, N. of Broken Hill, 1.iv.1915 (*H. C. Dollman*), type, female, in British Museum. Belgian Congo, 10 miles S.W. of Elizabethville, 18.iii.1928 (*Dr. H. S. Evans*), type male, and two others in British Museum (Natural History).

Note.—In immature specimens the elytra are brownish.

81. *P. aethiopicus* Bernhauer.

Bernhauer, 1915, *Ann. Mus. nat. Hung.* **13**: 142.

The structure of the aedeagus can be seen from figs. 138, 139, and calls for no special comment. The paramere, as figured in the lateral view, has been pulled away from the median lobe.

82. **P. rapaciosus** sp. n.

Black; mouth parts dark reddish brown; antennae pitchy black, with the first segment brownish and the last two segments light yellow; anterior and intermediate femora and tarsi pitchy brown.

The head of the unique specimen is very much damaged, but apparently it is strongly transverse, oval, with small flat eyes occupying about half the sides of the head; sides behind eyes convergent and rounded; posterior angles strongly rounded; on each side there are two interocular punctures, the outer one being situated as close to the marginal puncture of the eye as to the inner one, which is widely distant from the inner one of the other side; there is another pair on each side behind the interocular punctures, the inner punctures of which are situated more towards the base of the head than the outer punctures; several small punctures close to the anterior marginal punctures of the eyes, and several others in the postocular region.

Antennae short; third segment a little longer than the second; fourth to tenth decreasing in length, transverse, the penultimate segments strongly so.

Thorax slightly longer than broad ; anterior margin rounded, convex ; anterior angles marked, obtuse ; sides straight, feebly narrowed in front ; posterior angles broadly rounded with the base ; discal series each consisting of six more or less equidistant, large punctures.

Scutellum closely and finely punctured.

Elytra scarcely broader than the thorax, broader than long, parallel-sided, convex ; surface shining ; punctures rather fine and sparse.

Abdomen at base finely and moderately closely punctured, at apex very finely and very sparsely punctured.

Posterior tarsi with the first segment scarcely as long as the fifth, as long as the second and third together.

Length : 9 mm.

Male : The anterior tarsi moderately broadly dilated ; the aedeagus has the paramere very short and rounded at the apex ; the median lobe, viewed from above, is narrowed to a point at the apex ; viewed laterally it has a small hook on the outer side (figs. 140, 141).

Lulua : Kapanga, iii.1933 (*G. F. Overlaet*), type, unique male, in the Musée du Congo Belge.

83. **P. basipennis** sp. n. √

Head black ; thorax red ; elytra black at base, red at apex, the red colour extending almost to the scutellum in the centre, but not quite so far at the sides ; abdomen pitchy, apex of basal segments brownish red, this light margin being very narrow in the first visible segment and increasing towards the apex, until in the last visible segment it entirely covers it ; antennae black with the first two segments dirty brown and the last pitchy ; mouth parts brownish ; legs testaceous brown.

Head round, a little longer than broad ; eyes moderately small, their longitudinal diameter being a little greater than the length of the sides of the head behind eye measured as far as the bristle ; the anterior juxta-ocular puncture on each side double, the inter-ocular punctures quite close to it ; a puncture on each side close to the posterior juxta-ocular puncture ; three distinct punctures between the neck and the eye parallel to the margin of the head, and a few small punctures in the extreme hind angles ; surface shining with a very weak ground sculpture.

Antennae long, much longer than the head and thorax together ; third segment a little longer than the second ; fourth to seventh longer than broad, but not strongly so ; eighth to tenth subquadrate.

Thorax much wider than the head, longer than broad, widest behind, strongly narrowed in front ; front margin feebly rounded ; anterior angles strongly rounded ; sides almost straight ; posterior angles rounded with the base in a broad curve ; discal series each consisting of six, not very deep, equidistant punctures ; laterally with two pairs of punctures placed obliquely ; marginal punctures few but large.

Scutellum very finely, moderately closely punctured.

Elytra wider than the thorax, parallel-sided, longer than together broad, rather flat ; puncturation close and fine ; pubescence close, short, yellowish.

Abdomen more closely and finely punctured than the elytra.

Posterior tarsi fairly long ; first segment as long as the fifth, about equal to the second and third together.

Length : 6 mm.

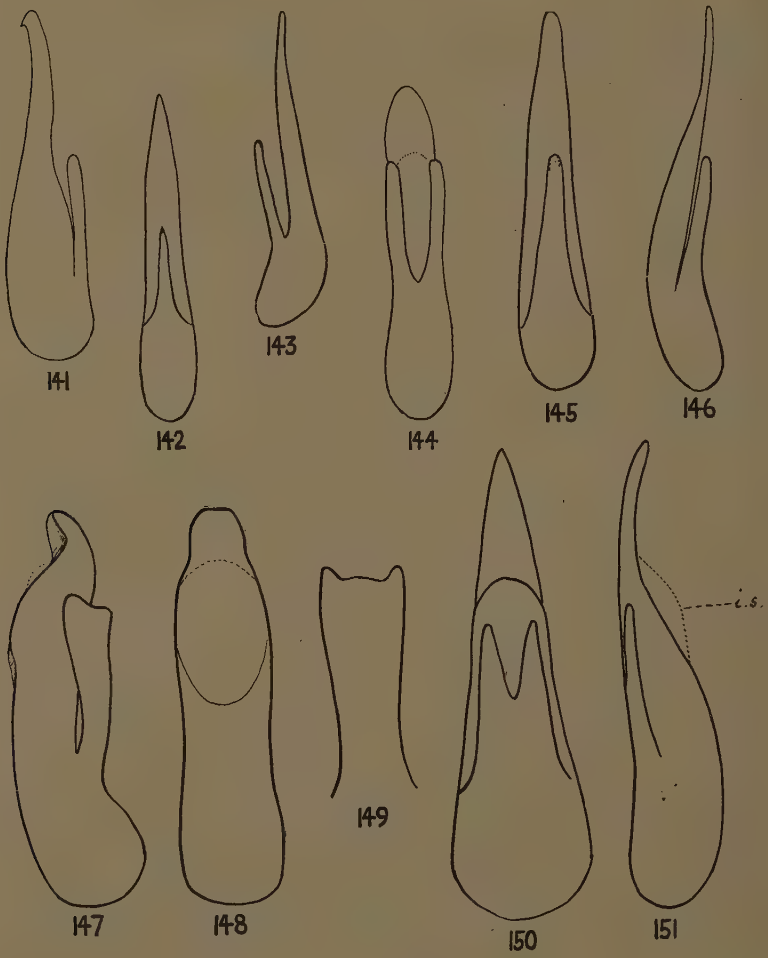
Male : Anterior tarsi moderately dilated ; the aedeagus is shown in figs. 142, 143.

N.W. Rhodesia : Namwaca, iii.1913 (*H. C. Dollman*), type in the British Museum (Natural History). N.W. Rhodesia : Mwengwa, 22.vii.1913 (*H. C. Dollman*), also in the British Museum.

84. *P. fimbriolatus* Erichson.

Erichson, 1840, *Gen. Spec. Staph.* : 486.

The aedeagus has a furcate paramere whose two branches are nearly parallel but rather widely separated from one another. (Fig. 144.)



FIGS. 141–151.—(141) *P. rapaciosus* sp. n. Aedeagus, lateral view. (142) *P. basipennis* sp. n. Aedeagus, upper view. (143) *P. basipennis.* Aedeagus, lateral view. (144) *P. fimbriolatus* Erichson. Aedeagus, upper view. (145) *P. nigriceps* Eppelsheim. Aedeagus, upper view. (146) *P. nigriceps.* Aedeagus, lateral view. (147) *P. gerardi* Bernhauer. Aedeagus, lateral view. (148) *P. gerardi.* Median lobe, lower view. (149) *P. gerardi.* Paramere. (150) *P. burgeoni* Bernhauer. Aedeagus, upper view. (151) *P. burgeoni.* Aedeagus, lateral view.

85. *P. nigriceps* Eppelsheim.

Eppelsheim, 1885, *Dtsch. ent. Z.* **1885** : 112.

There is nothing remarkable to note about the aedeagus of this species, as may be seen from figs. 145, 146. It must be pointed out, however, that there are in museums two distinct, though closely allied, species doing duty for *nigriceps* Eppelsheim, and it would require comparison with the type to decide which is the true species of that name.

86. *P. gerardi* Bernhauer.

Bernhauer, 1928, *Wien ent. Ztg.* **45** : 108.

As may be seen from figs. 147–149 the aedeagus is peculiar both for the curious formation of the apex of the median lobe and also for the shape of the paramere.

87. *P. burgeoni* Bernhauer.

Bernhauer, 1928, *Wien ent. Ztg.* **45** : 107.

In the upper view the median lobe is gradually narrowed from base to apex, but in the lateral view it is bent into a long, narrow, pointed portion at the apex. The paramere is nearly as broad as the median lobe and is triangularly furcate at the apex. The branches of the fork envelop the median lobe so that in the lateral view of the aedeagus the paramere does not conceal the outline of the median lobe. (Figs. 150, 151).

88. **P. orcinus** sp. n.

A small species, very similar in general appearance to *Gabrius nigritulus* Gravenhorst.

Black, elytra pitchy brown, antennae with the first two segments light reddish brown, legs light reddish-brown.

Head orbicular, very slightly broader than long (male); sides behind eyes nearly parallel for about half their length, then gradually narrowed in a curve to the neck; front of head broad; eyes very small, about half the length of the sides of the head behind eyes. Interocular punctures shallow, about twice as distant from one another as from the eyes; behind them a more or less transverse row of four weak punctures, the two middle punctures of which are a little posterior to the two outer punctures and about as distant from one another as from the eyes; a number of rather large shallow punctures scattered in the postocular region and near the base of the head.

Antennae with the second and third segments subequal, fourth a little longer than broad, fifth to tenth slightly transverse, eleventh shorter than the two preceding together.

Thorax distinctly longer than broad, a little narrower than the head (male); anterior angles rather marked, obtusely rounded; posterior angles less obtusely rounded with the base; front margin convexly rounded; discal series each consisting of six rather strong punctures.

Scutellum very finely punctured.

Elytra much shorter than together broad, shorter than the thorax; strongly, irregularly and not very closely punctured.

Abdomen very finely punctured.

Posterior tarsi with the first segment shorter than the fifth, scarcely as long as the second and third together.

Length: 5 mm.

Male: Eighth sternite feebly triangularly emarginate at apex, with a deep triangular depression before the emargination. Aedeagus with the median lobe gradually narrowed from base to apex in the upper view, slender at the apex in the lateral view; paramere simple, very short and slender, with a few indistinct pegs at extreme apex (figs. 152, 153).

Type, unique male, in the Musée du Congo Belge; Kivu: Lulenga, ix.1932 (*L. Burgeon*).

89. *P. turbidus* Erichson.

Erichson, 1840, *Gen. Spec. Staph.*: 484.

The very characteristic aedeagus of this species is shown in figs. 157–159. In the upper view the real apex of the median lobe cannot be seen as it is bent down almost at a right angle, as may be understood from fig. 157. The paramere is forked, and the inner margins of each branch are closely studded with very small pegs for nearly the whole of their length.

Specimens of this species are not rare in which there are more than six punctures in one or both of the discal series of the thorax.

90. *P. chapmani* Bernhauer.

Bernhauer, 1939, *Mém. Mus. nat. Hist. nat. Paris* (n.s.) **9**: 89.

The aedeagus, which is shown in figs. 155, 156, is very similar to that of *P. orcinus* sp. n., but the median lobe is much longer and the paramere is relatively broader.

It is not possible to say whether the following species should be in group 4 or group 5, as the thoracic series are abnormal in the unique type.

91. **P. hargreavesi** sp. n.

Black; antennae pitchy brown for the three basal segments, dull pale yellowish brown for the remainder; legs, including coxae, yellowish brown.

Head roundish, a little broader than long, broadest across the eyes, narrower behind; front broadly rounded; sides feebly curved, convergent posteriorly; hind angles rather obtusely rounded; base concave; eyes small, their length equal to that of the sides behind the eyes measured to the bristle, which is rather forward. Head very broadly, shallowly, depressed over nearly the whole width between the eyes, the depression extending a considerable distance longitudinally as well; interocular punctures widely separated, situated in the corners of the depression; another pair, equally distant, near the hind angle of the eye, several other distinct punctures in the postocular and basal regions.

Mandibles very long and slender.

Antennae very short; second and third segment about equal; fourth and fifth a little longer than broad; sixth quadrate; seventh to tenth transverse.

Thorax narrower than the head; surface very convex; anterior margin rounded; anterior angles very obtusely rounded; sides parallel; posterior angles obtusely rounded with the base; thorax about as long as broad; discal series consisting of six punctures in the right series and five in the left; the left series is very irregular, and probably five is the normal number; side margins with a number of distinct outstanding hairs.

Scutellum glossy, very finely and sparingly punctured.

Elytra together much broader than the thorax, broader than long; very finely, rather diffusely punctured; surface very shining; pubescence grey, very fine and long.

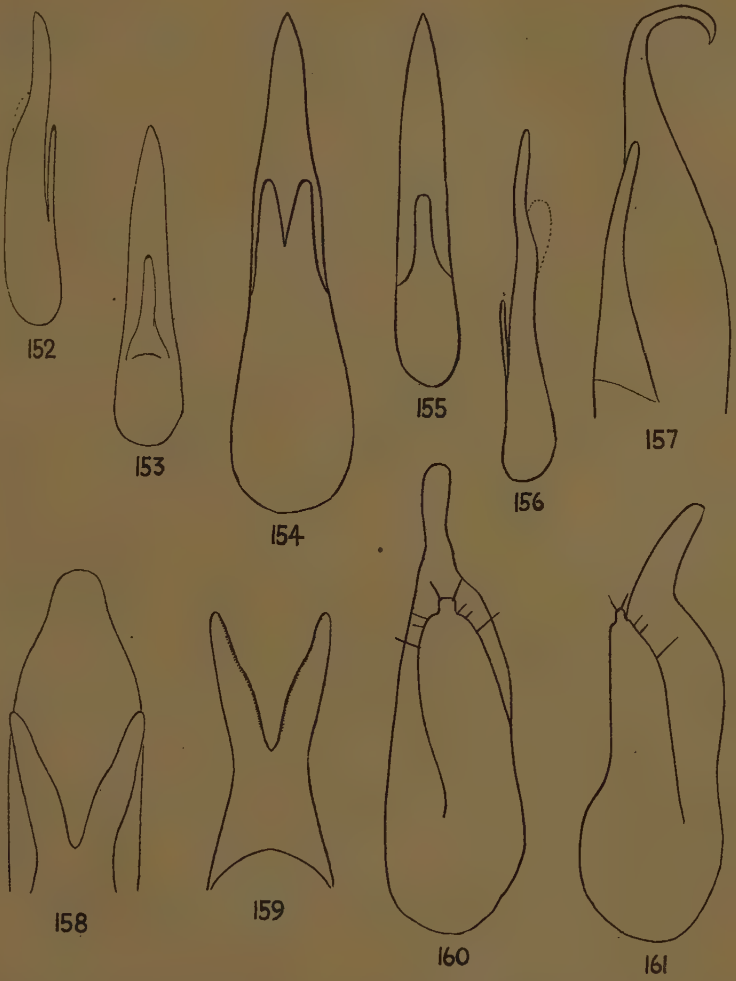
Abdomen extremely finely, rather sparingly punctured.

Length: 5·5 mm.

Male: Anterior tarsi simple; eighth sternite very narrowly, not very deeply excised in a pointed triangle, the excision filled with a membrane; the aedeagus has the median lobe long and pointed; the paramere is triangularly furcate (fig. 154).

Sierra Leone: Njala, x.1935 (*E. Hargreaves*), type, unique male, in the British Museum (Natural History).

This species is very much of the same build as *P. motoensis* Cameron, but is easily distinguished by the thoracic series of punctures and by the fine, diffuse punctuation of the elytra.



Figs. 152–161.—(152) *P. orcinus* sp. n. Aedeagus, lateral view. (153) *P. orcinus.* Aedeagus, upper view. (154) *P. hargreavesi* sp. n. Aedeagus, upper view. (155) *P. chapmani* Bernhauer. Aedeagus, upper view. (156) *P. chapmani.* Aedeagus, lateral view. (157) *P. turbidus* Erichson. Apex of aedeagus, lateral view. (158) *P. turbidus.* Apex of aedeagus, upper view. (159) *P. turbidus.* Paramere, inner face. (160) *P. gongulus* sp. n. Aedeagus, lateral view. (161) *P. gongulus.* Aedeagus, upper view.

Group 6.—*Discal Series of Thoracic Punctures Each Consisting of more than Six Punctures.*

92. *P. conradti* Bernhauer.

Bernhauer, 1912, *Ent. Mitt.* 1 : 206.

There is nothing remarkable about the aedeagus of this species (see figs. 174, 175). The paramere is only slightly longer than the median lobe, which is rounded at the apex. The pegs appear to be few in number.

93. **P. gongulus** sp. n.

A very distinct species, easily recognized by the extraordinarily dilated sides of the elytra at the apical angles, as well as by the large head and 8-punctate discal series of the thorax, and by the unusual shape of the aedeagus.

Black ; elytra brown, lighter at the extreme apical margins ; apical margins of the abdominal segments brown ; antennae black, basal segments brown, base of the second red ; legs, including coxae, brown, femora lighter, tibiae infuscate.

Head nearly rectangular, distinctly transverse ; front nearly straight but with a small portion in the centre distinctly produced and rounded ; sides from behind the eyes to the bristle nearly straight and parallel ; posterior angles very obtusely rounded ; base concave ; eyes very small, slightly less than the sides behind measured to the bristle ; the punctures on the head in the unique type differ on each side ; there are, however, two pairs of interocular punctures, one pair level with the anterior margins of the eyes, the other level with the middle of the eyes ; halfway between each of these and the eye is another puncture ; several distinct punctures in the postocular region, especially between the eye and the neck ; a much larger puncture and one or two smaller ones near the base towards the centre of the head ; there is a tendency for the punctures to form two longitudinal lines on each side not far from the margin of the eye ; there is also a distinct depression in the middle of the head in front ; ground sculpture consisting of close lines, which are transverse on the basal half.

Antennae as long as the head and thorax together ; second segment about as long as the first ; third longer than the second ; fourth to tenth increasing in width, decreasing in length ; fourth and fifth a little longer than broad ; sixth quadrate ; seventh to tenth a little transverse ; eleventh short.

Thorax narrower than the head (male), longer than broad ; anterior margin rounded ; anterior angles obtuse ; sides straight, parallel ; posterior angles rounded with the base in a large curve ; ground sculpture of close transverse scratches ; discal series each consisting of eight punctures, the second, third and fourth closer together than the rest, fifth, sixth and eighth increasing in distance apart, seventh out of line with the others, situated externally to the series ; this puncture may be abnormal, but it is exactly the same on each side in the unique type ; usual lateral punctures.

Scutellum distinctly punctured.

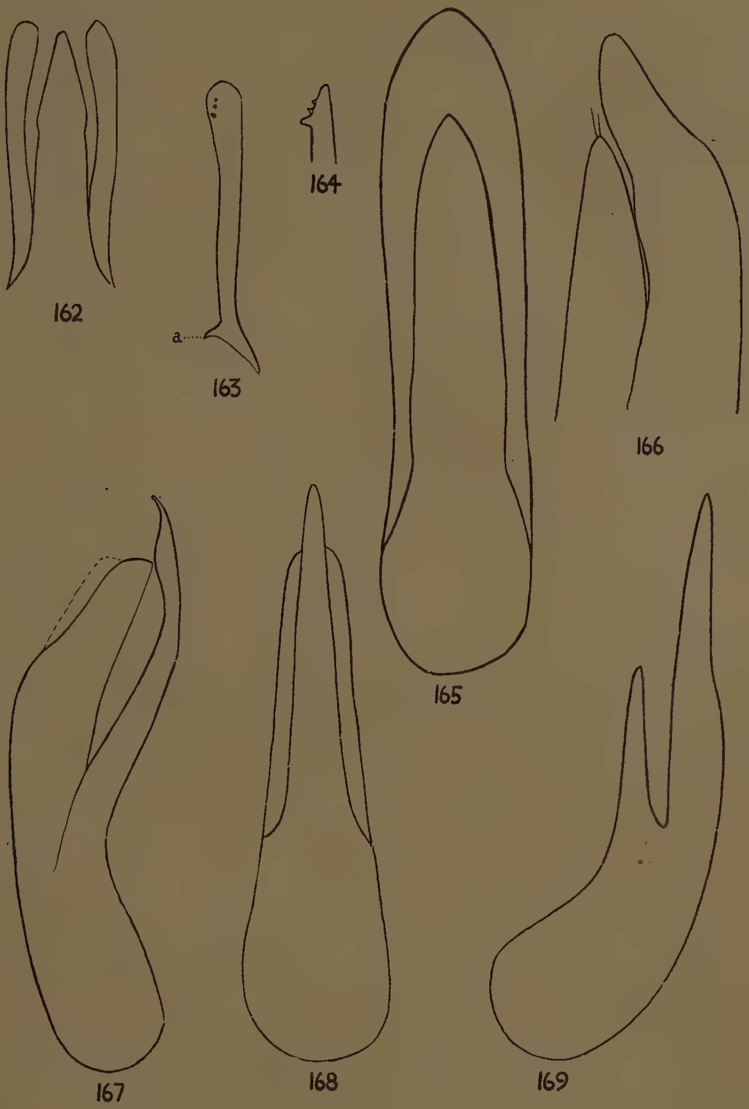
Elytra at base wider than the thorax ; sides distinctly divergent posteriorly for half their length, then strongly inflated and rounded to the marked posterior angles ; basal margin of each elytron straight near the suture and feebly rounded to exterior angle ; puncturation very close and moderately strong, rather irregular ; pubescence short, fine, light.

Abdomen closely and finely punctured, more sparingly towards the apex.

Posterior tarsi with the first segment shorter than the fifth, shorter than the second and third together.

Length : 6 mm.

Male : The aedeagus is remarkable for its peculiar form ; the median lobe is strongly bent at the apex on its outer surface ; it is prolonged at the apex for a considerable length ; the paramere is asymmetrical and asymmetrically situated on the median lobe ; this, too,



FIGS. 162–169.—(162) *P. biparamerosus* sp. n. Apex of aedeagus, upper view. (163) *P. biparamerosus*. Paramere. (164) *P. biparamerosus*. Apex of paramere, lateral view. (165) *P. ocypoides* Schubert. Aedeagus, upper view. (166) *P. ocypoides*. Apex of aedeagus, lateral view. (167) *P. aemulus* Tottenham. Aedeagus, lateral view. (168) *P. aemulus*. Aedeagus, upper view. (169) *P. lucanicornis* Bernhauer. Aedeagus, lateral view.

has a distinct projection at the apex, but very short; the form can be appreciated from figs. 160, 161.

KIVU: N'Gama, i.1926 (*H. Schouteden*), type, unique male, in the Musée du Congo Belge.

94. **P. tamulus** sp. n.

Black; elytra slightly pitchy; abdomen rather iridescent and a little brownish towards apex; legs pitchy with femora a little lighter.

Head transverse, rather oval, much broader than long; front very little produced before eyes, nearly straight in middle; eyes flat, moderate in length, slightly longer than the sides behind eyes; sides scarcely rounded, scarcely convergent behind; posterior angles very obtusely rounded; base straight; four punctures placed transversely between the eyes, the distance between the inner two being equal to that between the bases of the antennae, the outer punctures being midway between the inner punctures and the marginal punctures of the eyes; one or two much smaller, shallow punctures behind these, and a few diffuse punctures in the postocular region; ground sculpture very weak and close.

Antennae long and rather slender, longer than the head and thorax together; second and third segments about equal; fourth not much shorter than the third and much longer than broad; fourth to tenth decreasing in length, but all distinctly longer than broad, most of them much so.

Thorax broader than the head, broader than long, broader behind than in front; anterior margin truncate; anterior angles strongly deflexed, a little obtusely rounded; sides straight, divergent posteriorly; posterior angles rounded with the base; discal series irregular, more or less double or treble, consisting of three or four not large punctures and some five or six very small but distinct punctures; other similar small and one or two larger punctures diffusely scattered over the whole of the lateral area; it is difficult to state the exact number of punctures in the discal series owing to their irregular nature; ground sculpture as on the head.

Scutellum large and broad, very finely, rather diffusely, punctured.

Elytra very finely, rather closely punctured, with several distinctly larger punctures more or less disposed in indistinct longitudinal rows; a little broader than the thorax, broader than long, wider behind.

Abdomen very finely and scantily punctured, the punctures being in two or three transverse rows on each segment.

Posterior tarsi with the first segment scarcely longer than the fifth, equal to the second and third together.

Length: 9 mm.

KIVU: Tshibinda, xi.1932 (*L. Burgeon*), type, unique female, in the Musée du Congo Belge.

The peculiar thoracic puncturation makes this insect distinct, together with the finely punctured elytra and smooth abdomen, and the large accessory elytral punctures.

95. **P. biparamerosus** sp. n.

This species is of exceptional interest, since the aedeagus possesses two parameres; that fact, coupled also with its long, slender, falciform mandibles, and the puncturation of the thorax and the exceptionally long elytra, seems to warrant a distinct subgenus, for which I propose the name **Sectophilonthus** with *P. paramerosus* as its genotype.

The species may easily be distinguished, apart from the form of the aedeagus, by its falciform mandibles, its very long, shining, finely punctured elytra, and by the puncturation of the thorax, which consists of exceptionally fine punctures, the discal series being numerous and irregular, and there being numerous irregular similar punctures scattered all over the lateral region.

Black; head, thorax and elytra very shining, abdomen not so shining; antennae brown, with basal and apical segments lighter; all the abdominal segments narrowly reddish brown on the apical margins; femora red-brown.

Head rather quadrate; eyes a little shorter than the margins of the head behind eyes; sides feebly divergent behind; posterior angles strongly rounded, rather bulging; anterior marginal puncture of the eye situated a little distance from the margin; interocular punctures appreciably more distant from one another than from the marginal punctures of the eyes; a few punctures scattered in the postocular region; all the punctures on the head very minute and indistinct. Maxillary palpi with the last segment rather short, a little longer than the penultimate, which is stout. Mandibles very long and falciform.

Thorax, at its greatest width, fully as wide as the head, slightly narrowed behind, front margin strongly convex, anterior angles obtusely rounded, posterior angles less obtusely rounded, rounded with the base. All the punctures on the thorax are very minute and their arrangement is dissimilar on the two sides; the discal series on the left consists of eight punctures irregularly spaced, the right series consists of ten punctures, several of which are out of line; there are quite a number of similar punctures outside the discal series, which show a tendency to align themselves parallel to the discal series, especially on the right side, which I believe is more representative of the normal in the species.

Elytra as wide as the thorax, very long, finely, not very closely punctured.

Abdomen more closely punctured than the elytra, the punctures on the basal segments being about equal to those on the elytra, those on the apical segments being stronger.

Antennae about as long as head and thorax together; second segment stout at apex, but longer than broad, third distinctly longer than second, the rest subequal, all longer than broad, and all distinctly widened apically; eleventh shorter than ninth and tenth together.

Greater part of the legs missing.

Length: 7·5 mm.

Male: Sternite eight with the apical margin very feebly emarginate in a curve for its whole width; aedeagus remarkable for possessing two parameres. A paramere is shown in fig. 163; it just touches the other paramere at (*a*), but the two are only connected by the membrane which joins them to the median lobe; distally there are three tooth-like pegs on each, which are outstanding if the paramere is viewed laterally (fig. 164). Apparently they have their faces slightly concave and directed towards the median lobe, so that they do not show the true contour of their apical margins in the position shown in fig. 162, when still attached to the median lobe.

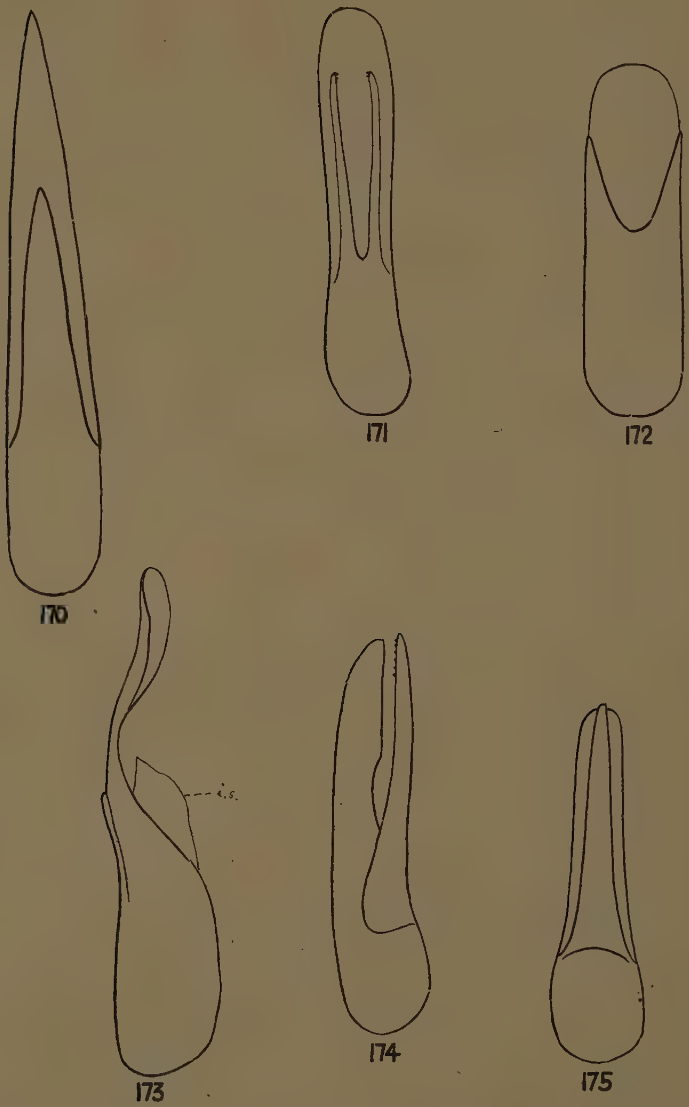
Type, unique male, MADAGASCAR: Tananarive, in my collection.

Group 7.—*Species of Large or Moderate Size; Head Usually Black, Thorax, Elytra and Abdomen Brown, Reddish Brown or Yellowish Brown.*

This is purely a group of convenience, based on the prevailing colour. There are a few similarly coloured small species, (*rufescens* Bernhauer, *volvulus* Bernhauer, *sanguineus* Fauvel) which I have included in other keys according to the number of punctures in the discal series of the thorax. In the species considered below, I have used the discal series in the key, but I have not taken the numbers of these punctures as a characteristic of the whole group. Since there is only one new species to be described in this group I have condensed descriptions of the various species and included these descriptions in the key.

Key to the Species.

1. Body not unusually broad . . . . 3.
Body very broad . . . . 2.



Figs. 170–175.—(170) *P. lucanicornis* Bernhauer. Aedeagus, upper view. (171) *P. bidentiformis* sp. n. Aedeagus, upper view. (172) *P. dollmani* Bernhauer. Aedeagus, upper view. (173) *Gabrius monticola* Bernhauer. Aedeagus, lateral view. (174) *P. conradti* Bernhauer. Aedeagus, lateral view. (175) *P. conradti*. Aedeagus, upper view.

2. Size large, 15 mm.; head very strongly transverse, with front very much produced in a curve; eyes occupying nearly the whole of the sides of the head; thorax strongly transverse; discal series of six punctures, of which the sixth is equidistant from the fifth and from the base; elytra strongly transverse, moderately and closely punctured; abdomen very finely, not very closely punctured; upper surface shining; antennae with segments four to ten serrate. Habitat in Nigeria . . . . 96. *cervicornis* Schubert.

Size large, 12–15 mm.; head more than twice as broad as long; eyes fully three times as long as the sides of the head behind eyes; thorax nearly twice as broad as long; discal series of five fine punctures, of which the fifth is remote from the rest; elytra scarcely longer than the thorax, finely punctured, with some larger punctures; abdomen finely, fairly thickly punctured. Habitat in Belgian Congo
97. *grandis* Bernhauer.

3. Discal series of thorax consisting of five or more punctures . . . . 4.

Discal series of thorax consisting of four punctures; antennae relatively short, scarcely serrate, the serrate segments about as wide at apex as long; head strongly transverse, not produced in front, with eyes moderate, and sides behind eyes parallel; thorax deep reddish brown, distinctly transverse; elytra finely and evenly punctured, scantily pubescent, as long as together broad, flat, longer than the thorax; abdomen very finely and very closely punctured; anterior tarsi in male very broadly dilated; aedeagus, figs. 165, 166. Habitat in Rhodesia, Belgian Congo . . . . 98. *ocypoides* Schubert.

4. Size smaller, 8–12 mm.; colour often light yellowish brown; antennal segments if serrate not distinctly longer than broad . . . . . 5.

Size larger, 15 mm.; colour dark reddish brown, rather dull; antennae very long, segments longer than broad, distinctly serrate, but with their bases relatively broad; head transverse, rather angularly produced in front; eyes large, occupying three-quarters of the sides of the head; sides behind eyes convergent and rounded; thorax scarcely transverse, sides converging anteriorly, discal series each consisting of six punctures (or more); elytra convex, together broader than long, closely and finely punctured, with long close pubescence; abdomen finely, fairly closely punctured, very pubescent; anterior tarsi of male moderately dilated; aedeagus, figs. 167, 168. Habitat in Tanganyika . . . . 99. *aemulus* Tottenham.

5. Segments of antennae not serrate, eighth to tenth transverse . . . 6.

Segments of antennae very strongly serrate, very wide at apex and narrow at base; head strongly transverse, scarcely produced in front; eyes large, convex, occupying three-quarters of the sides of the head; thorax very strongly transverse; discal series each consisting of six (or more) fine punctures; elytra broader than long, moderately punctured; scutellum very finely and closely punctured, more finely and more closely than the elytra; abdomen light yellowish brown with strong golden iridescence and with ill-defined blackish patches at the bases of the segments, punctures fine and moderately close; aedeagus, figs. 169, 170. Habitat in Rhodesia.
100. *lucanicornis* Bernhauer.

6. Discal series of thorax each consisting of six punctures . . . . . . 7.

Discal series of thorax each consisting of five punctures; antennae with the basal segments brown, the rest dark; head transverse, oval; eyes small, occupying less than half of the sides of the head; head behind eyes nearly parallel-sided, slightly rounded; hind angles very broadly rounded; punctures strong; thorax transverse, sides but slightly convergent anteriorly; discal series of large and equidistant punctures; base flatly rounded; elytra a little broader than the thorax, longer than broad, moderately and not very closely punctured, pubescence scanty; abdomen punctured nearly as strongly as the elytra, but closer at the bases of the segments, more sparingly at the apices, very sparingly at the extreme apex; aedeagus fig. 171. Habitat in Madagascar. (Type, male, in my collection) . 101. **bidentiformis** sp. n. ✓

7. Antennae with the penultimate segments scarcely serrate, eleventh segment lighter than the rest; head scarcely transverse, a little produced in front, eyes moderate, occupying two-thirds of the sides of the head; thorax slightly longer than broad, sides nearly parallel, slightly convergent anteriorly, base strongly rounded; elytra as long as together broad, moderately punctured; scutellum punctured almost like the elytra; abdomen reddish-brown, darkly iridescent, very finely and very closely punctured; aedeagus, fig. 172. Habitat in Rhodesia . . . . 102. *dollmani* Bernhauer.

Antennae with the eleventh segment more definitely lighter, penultimate segments more transverse; head less transverse, hind angles more marked, eyes smaller; thorax narrower, discal series of punctures closer; elytra more sparingly punctured; abdomen much more sparingly punctured. Habitat in Madagascar. 103. *laticornis* Bernhauer.

References to species in this group:

96. *P. cervicornis* Schubert, 1911, *Dtsch. ent. Z.* **1911** : 25.
97. *P. grandis* Bernhauer, 1932, *Rev. Zool.-Bot. afr.* **22** : 147.
98. *P. ocypoides* Schubert, 1911, *Dtsch. ent. Z.* **1911** : 22.
99. *P. aemulus* Tottenham, 1939, *Proc. R. ent. Soc. Lond.* (B) **8** : 233 nom. nov.
    = *P. serraticornis* Bernhauer, 1908, *Denkschr. med.-naturw. Ges. Jena* **13** : 110.
100. *P. lucanicornis* Bernhauer, 1908, *ibid.*, **13** : 111.
102. *P. dollmani* Bernhauer, 1934, *Rev. Zool.-Bot. afr.* **24** : 236.
103. *P. laticornis* Bernhauer, 1906, *Dtsch. ent. Z.* **1906** : 190.

In this group should also be included the following species which are unknown to me, and which I was unable to include in the key from the descriptions alone:

P. subtilicornis Bernhauer, 1932, *Rev. Zool.-Bot. afr.* **22**: 148 (Belgian Congo).
P. rufus Fauvel, 1898, *Rev. Ent.* **17** : 184 (Madagascar).
P. pollux Fauvel, 1905, *ibid.*, **24** : 178 (Madagascar).

P. rufus has six punctures in the discal series of the thorax, while the other two species each have five punctures.

104. *Gabrius monticola* Bernhauer.

Bernhauer, 1931, *J. Linn. Soc. Lond.* (*Zool.*) **37** : 586.

The aedeagus of this species is shown in fig. 173.

Vol. 100. Part 13. Pp. 363–391, 118 figs. 30th December, 1949

Eu. 344

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CONTENTS

PAGE

DIRSH, V. M., D.Sc. The genus *Thalpomena* Saussure, 1884 (Orthoptera, ACRIDIDAE) and its allies . . . . 363–391, 118 figs.

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9. **Yorkshire Naturalists' Trust, Ltd.**
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THE GENUS *THALPOMENA* SAUSSURE, 1884 (ORTHOPTERA, ACRIDIDAE) AND ITS ALLIES.

By V. M. Dirsh, D.Sc.

(*Anti-Locust Research Centre, British Museum (Natural History)*).

Communicated by Dr. B. P. Uvarov, C.M.G.

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With 118 Text-figures.

The Genus *Thalpomena* was described by Saussure in 1884 for *Oedipoda algeriana* Lucas, 1849, and for two new species *Thalpomena persa* and *Th. ledereri*.

The present study has shown that *persa* and *ledereri* are generically distinct from *algeriana*, which has been designated by Kirby (1910) as the type of the genus *Thalpomena*. This genus includes several species from North-West Africa.

Th. persa and *ledereri* proved to belong to the genus *Pseudoceles* described by I. Bolivar in 1899 for a species from Asia Minor and incorrectly synonymized by Uvarov in 1930 with *Thalpomena* Saussure. To this genus belong several species occurring in Western Asia.

Thalpomena hirtipes Uvarov, 1923, is so distinct from both *Thalpomena* and *Pseudoceles* that a new genus *Crinita* must be erected for it.

A quite distinct genus of this group is *Cophotylus* Krauss, 1902, based on a single species from Arabia. To this genus are referred also *Thalpomena splendens* Uvarov, 1933 (Baluchistan) and *Wernerella aurora* Karny, 1907 (Sudan), as well as a new species from Persia. This genus is not very homogeneous and is possibly nearer to *Sphingonotus* Fieber than to *Thalpomena*.

This whole group of genera is associated in its distribution with low dry mountains, its members occurring on stony screes and bare rocks. This leads to a strict localization of populations and results in the formation of numerous species and lower taxonomic groups, which remain in isolation. Therefore, almost every locality and every population represents a distinct taxonomic group, often of very uncertain status. Extensive studies on as many as possible of such local populations are necessary before their status and interrelation can be understood. In the meantime, great caution has been exercised in establishing species and subspecies, and further work may show the need for their subdivision.

Oedipoda maderae Serville, 1839, from Madeira, has been referred by Kirby (1910) to the genus *Thalpomena*, but the original description is insufficient for this, and the type appears to have been lost. Therefore, this species must remain doubtful.

TRANS. R. ENT. SOC. LOND. 100. PART. 13. (DEC. 1949).

I am grateful to Dr. B. P. Uvarov for his advice and help, and to Dr. R. Ebner (Vienna), Dr. L. Chopard (Paris) and Sr. E. Morales Agacino (Madrid) for the material they have sent for my studies.

Most of the material is in the collections of the British Museum (Natural History), where all the types are deposited, except where it is otherwise stated in the text.

All measurements, except where otherwise stated, are in millimetres.

Thalpomena Saussure. (Figs. 1, 7, 8, 12.)

1884, *Thalpomena* Saussure, *Mém. Soc. Genève* **28** : 184.
1910, *Thalpomena* Kirby, *Syn. Cat. Orthopt.* **3** : 245.

Type. *Thalpomena algeriana* (Lucas), designated by Kirby (1910, *l. c.*).

Of medium size, robust. Head in profile does not project above pronotum. Frons perpendicular, slightly convex. Frontal ridge shallowly sulcate, with raised margins, slightly constricted below the ocellus, narrowed at the apex. Foveolae of vertex distinct, concave, irregularly triangular. Fastigium of vertex elongate strongly concave, with sharp lateral carinae. Pronotum without constriction, flat above, lateral margins divergent backwards. Median carina linear, fine, slightly raised in front of the first sulcus. Three transverse sulci. Posterior angle of metazona right or acute. Elytra short, broad; apex obliquely truncate; reticulation dense; vena intercalata sinuate, at the apex approximating and almost touching vena radialis posterior. Wing very broad, with strongly convex external margin; basal disc coloured, usually with a dark fascia. Hind femur short and broad. Subgenital plate of the male short, obtusely conical at the apex. Ovipositor short, slender, valvae curved; lower valva with a projection on the external margin.

Key to species of *Thalpomena*.

1 (6). Fastigium of vertex broad, as wide as long, with short carinae (figs. 15, 16, 17, 18, 20, 26).
2 (3). Median carina of pronotum in front of the first sulcus strongly convex (fig. 27). Lateral margins of metazona slightly divergent, almost parallel (fig. 28). Basal disc of wing bluish green . . . . *viridipennis* Uvarov.
3 (2). Median carina of pronotum weakly convex or straight (figs. 21, 37). Lateral margins of metazona strongly divergent (figs. 22, 38). Basal disc of wing pink or azure blue.
4 (5). Carinae of fastigium gradually curved with rounded or obtuse angles (figs. 15, 16, 17, 18, 20). Lateral margins of prozona between sulci not gibbose (fig. 22). Basal disc of wing pink *algeriana* (Lucas).
5 (4). Carinae of fastigium sharply curved, with acute angles (fig. 26). Lateral margins of prozona between sulci gibbose (fig. 38). Basal disc of wing greenish blue . . . . *coeruleipennis* Finot.
6 (1). Fastigium narrow, two or three times as long as broad, with long carinae (figs. 19, 25, 33, 36).
7 (12). Metazona slightly broader than prozona (figs. 35, 41), with lateral margins moderately divergent.
8 (9). Median carina of pronotum slightly convex in front of the first sulcus (fig. 34); lateral margins of prozona between sulci not gibbose (fig. 35), of metazona smooth and straight. Basal disc of wing azure blue . . . . *azureipennis* Uvarov.

Measurements of Thalpomena *Species.*

Name.	Elytron.			Pronotum.			Hind femur.			Fastigium.
Males.	Length. (mm.)	Width. (mm.)	L./W.	Prozona. (mm.)	Metazona. (mm.)	Total. (mm.)	Length. (mm.)	Width. (mm.)	L./W.	Width. (mm.)
Thalpomena algeriana algeriana	15	3·5	4·3	1·3	2·4	3·7	9	3·3	2·7	0·9
Th. alg. intermedia	15–16	3·2–3·7	4·3–4·7	1·1–1·4	2·3–2·6	3·4–4	8·7–9·7	3–3·3	2·7–3	0·8–0·9
Th. alg. montana	14–15·5	3·2–3·5	4–4·7	1·2–1·3	2·2–2·7	3·5–4	8·3–9·4	3–3·3	2·7–3	0·8–0·9
Th. alg. maroccana	15–16	3·5–3·5	4·3–4·6	1·3–1·4	2·5–2·7	3·9–4·1	9·1–9·3	3–3·3	2·8–3	0·9–0·9
Th. viridipennis	14–16·5	3·5–3·8	4–4·6	1·2–1·4	2·1–2·9	3·3–4·2	8·4–10	2·7–3·5	2·4–3·1	0·7–0·9
Th. azureipennis	16–17	3·4–3·6	4·7–4·7	1·2–1·2	2·4–2·5	3·6–3·8	8·7–9·7	3·0–3·0	3–3·2	0·7–0·7
Th. deserta	15–16·4	3·2–3·5	4·6–5	1–1·3	2–2·4	3·2–3·7	8·6–9·3	2·7–3	3–3·2	0·7–0·8
Th. rungsi	16·5	3·5	4·7	1·3	2·7	4	9·8	3·1	3·3	0·7
Th. coerulescens	15·8–18	3–3·5	4·5–5·4	1–1·2	1·9–2·6	2·9–3·8	8–9·1	2·5–3	3·1–3·4	0·6–0·8
Females.										
Thalpomena algeriana algeriana	18·3	4·5	4·1	1·8	3·6	5·4	10·2	4·5	2·8	1·2
Th. alg. intermedia	18–21	4–4·5	4·3–4·7	1·5–1·8	3·2–3·5	4·7–5·3	10·7–12·2	3·7–4·3	2·9–3	1–1·1
Th. alg. montana	15–18·5	3·4–4·6	4–4·9	1·5–1·7	2·7–3·6	4·2–5·3	9·7–12·2	3·3–4·3	2·5–3	1–1·1
Th. alg. maroccana	18·5–19	4·5–4·5	4·2–4·2	1·5–1·7	3·1–3·5	4·6–5·2	10·9–11·4	3·6–3·9	2·8–3	1·1–1·2
Th. viridipennis	17·5–21	4·2–5·1	3·9–4·5	1·5–1·8	3–3·7	4·7–5·6	10·7–12	3·4–4·1	2·8–3·2	1·0–1·2
Th. azureipennis	21	4·7	4·5	1·6	3·5	5·1	10·1	4	2·9	1
Th. coeruleipennis	17	3·5	4·9	1·3	2·6	4	10	3·1	3·2	1
Th. deserta	18–21	3·5–4·6	4·5–5·2	1·3–1·5	2·1–3·8	3·5–4·7	9·5–11·9	3–3·9	2·9–3·3	0·9–1·1
Th. rungsi	18–20	4·5–4·5	4–4·4	1·5–1·7	3·1–3·1	4·6–4·8	10·4–11·6	3·6–4	2·9–2·9	1·1
Th. coerulescens	18–21	3·2–4	5–5·6	1·1–1·4	2·4–2·9	3·5–4·3	9·1–10·6	2·9–3·4	3·1–3·3	0·7–0·8

9 (8). Median carina of pronotum straight, scarcely raised between second and third sulci (fig. 40); lateral margins of prozona between sulci slightly gibbose (fig. 41), of metazona smooth and slightly convex. Basal disc of wing rose.

10 (11). Fastigium three times as long as broad (fig. 33). Coloration pale ochreous. Basal disc of wing light rose with an obsolescent fascia and ray . . . . **deserta** sp. n.

11 (10). Fastigium twice as long as broad (fig. 19). Coloration dark grey, almost black. Basal disc of wing rose, with distinct fascia without ray . . . . **rungsi** sp. n.

12 (7). Metazona distinctly broader than prozona (fig. 24), lateral margins strongly divergent. Basal disc of wing hyaline blue *coerulescens* Uvarov.

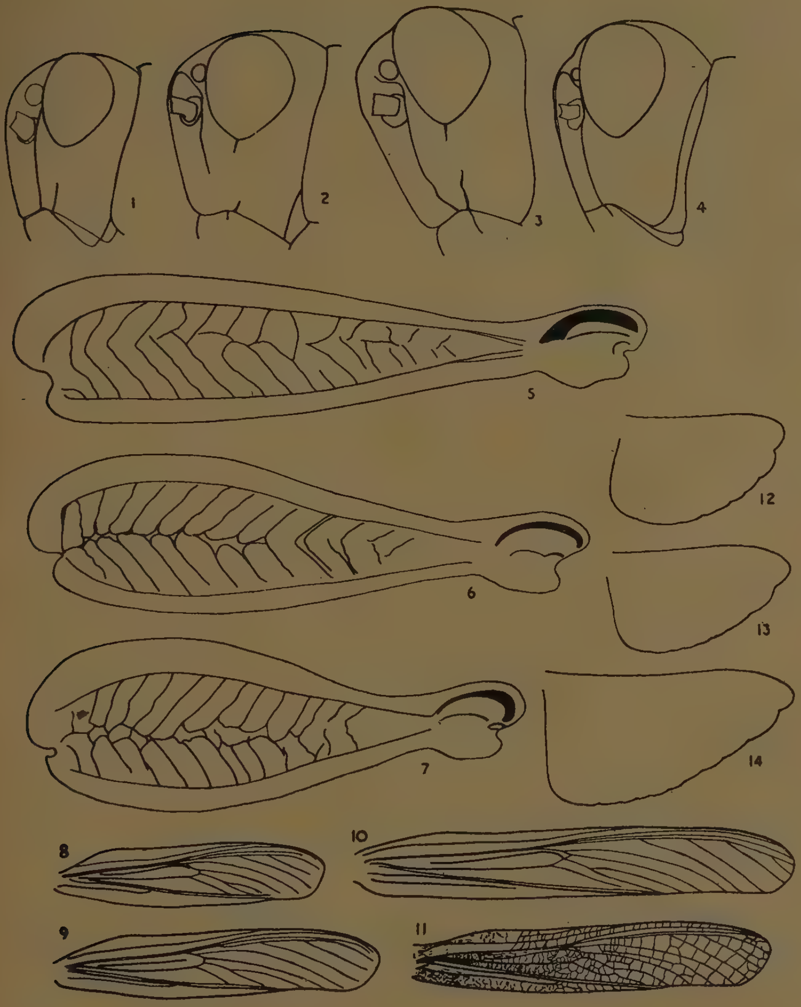
Comparative Characters of the Genera Thalpomena, Pseudoceles, Cophotylus *and* Crinit

Thalpomena.	*Pseudoceles.*	*Cophotylus.*	*Crinita.*
Head does not project above pronotum.	Head projects above pronotum.	Head strongly projects above pronotum.	Head strongly projec above pronotum.
Frons perpendicular, slightly convex.	Frons oblique, straight.	Frons strongly oblique, straight.	Frons strongly obliqu convex.
Prozona and metazona of pronotum flat and smooth. Median carina in profile interrupted by three sulci.	Prozona of pronotum subcylindrical, its lateral margin between sulci gibbose; metazona smooth. Median carina in profile interrupted by two sulci.	Prozona of pronotum subcylindrical, slightly constricted, its lateral margin between sulci less gibbose; metazona smooth. Median carina in profile interrupted by two or three sulci.	Prozona of pronotu constricted, its later margin between sul feebly gibbose; meta zona smooth. Media carina in profile inte rupted by three sulc
Elytron short, broad. Vena intercalata sinuate, at the apex approximating radialis posterior. Reticulation very dense.	Elytron broad and relatively long. Vena intercalata straight, parallel to radialis posterior. Reticulation dense.	Elytron long, narrow. Vena intercalata straight, sinuate. Reticulation not very dense.	Elytron long, narro Vena intercalata sinu ate, at apex approx mating radialis po terior. Reticulatio very sparse.
Wing short and broad, external margin strongly convex.	Wing short, less broad; external margin slightly convex.	Wing long, narrow; external margin straight.	Wing narrow; extern margin almos straight.
Hind femur short and broad.	Hind femur moderately slender.	Hind femur very slender.	Hind femur moderatel slender.

Thalpomena algeriana algeriana (Lucas). (Figs. 15, 21, 22, 29, 47, 49.)

1849, *Oedipoda algeriana* Lucas, *Expl. Alg.* **3** : 34.
1884, *Thalpomena algeriana* Saussure, *Mém. Soc. Genève*, **28** : 184.
1910, *Thalpomena algeriana* Kirby, *Cat. Orth.* **3** : 245.

♂. Very robust, particularly in the thorax. Frontal ridge feebly constricted below the ocellus, weakly narrowed to the apex. Fastigium broad, with strongly curved carinae. Pronotum above flat, long; lateral margins straight, divergent backwards. Median carina in profile almost straight. Metazona acutangulate, twice as long as prozona.



FIGS. 1–14.—(1–4) Head in profile: (1) *Thalpomena algeriana* (Lucas); (2) *Pseudoceles oedipodioides* I. Bol.; (3) *Cophotylus steindachneri* Krauss; (4) *Crinita hirtipes* (Uv.). (5–7) Hind femur: (5) *Cophotylus steindachneri* Krauss; (6) *Pseudoceles oedipodioides* I. Bol.; (7) *Thalpomena algeriana* (Lucas). (8–11) Elytron: (8) *Thalpomena algeriana*; (9) *Pseudoceles oedipodioides* I. Bol.; (10) *Cophotylus steindachneri* Krauss; (11) *Crinita hirtipes* (Uv.). (12–14) Wing: (12) *Thalpomena algeriana* (Lucas); (13) *Pseudoceles oedipodioides* I. Bol.; (14) *Cophotylus steindachneri* Krauss.

Lower margin of lateral lobe sinuate. Elytra short, broad, ratio of length to width 4·3; membrane hard, non-transparent. Wing short, broad, external margin very convex. Hind femur short, broad, ratio of length to width 2·7. Hind knee short, broad, with short upper lobe. Subgenital plate short, subconical, obtuse at the apex. Body not pilose.

Coloration dirty yellow; elytron with scattered small brown spots; wing at the base pink, with a dark narrow fascia and a narrow basal ray; apical lobes not darkened. Inner side of hind femur black, with pale fascia in front of the knee; above and outside with two indistinct dark fasciae. Hind tibia dirty yellow.

♀ (Cotype). As the male, but larger and more robust. Ovipositor short, valvae fine, strongly curved. Lower valve with large rounded projection on the external side.

Length of body, ♂ 16, ♀ 21; pronotum ♂ 37, ♀ 54; elytron, ♂ 15, ♀ 18·5; hind femur, ♂ 9, ♀ 12.

ALGERIA: Kouba, 1 ♀ (cotype). Alger, 1 ♂, 1 ♀.

The female, kindly presented to the British Museum by Dr. L. Chopard, is one of the long and very uniform series in the Paris Museum, used by Lucas when describing the species. This cotype made it possible to establish beyond doubt the subspecies *Thalpomena algeriana algeriana* (Lucas).

Thalpomena algeriana **intermedia** subsp. n. (Figs. 16, 30.)

♂ (Type). Less robust than *Th. alg. algeriana.* Fastigium of vertex broad, carinae more weakly curved than in the typical subspecies, but rather narrowed to the apex.

Coloration dirty yellow greyish. Elytron with small indistinct spots. Basal disc of wing hyaline rose; fascia broader, less clear; apical lobes obscure. In other respects as typical subspecies.

Length of body 14·5; pronotum 3·6; elytron 15; hind femur 9.

♀ (Paratype). Similar to male, but larger. Ovipositor as in *Th. alg. algeriana.*

Length of body 20·5; pronotum 5; elytron 18; hind femur 11.

ALGERIA: Oran, 5–8.x.1882, 2 ♂; 8–25.i.1883, 3 ♂ (including type); 25.i, 26.iii, 7.viii.1883, 5 ♀. Hammam Rhira, v.1908, v.1911, iv.1912, 13.v.1913, 2 ♂, 3 ♀ (*Rothschild and Hartert*). El-Gehra station, S. of Constantine, 2.viii.1939, 1 ♀. Boghari, 28.ix.1937, 1 ♀ (*M. N. Korsakoff*).

This subspecies includes intermediate forms connecting neighbouring subspecies. As a subspecies, *Th. alg. intermedia* is the least definite of all, but cannot be united with any other subspecies.

Thalpomena algeriana **montana** subsp. n. (Figs. 17, 31.)

♂ (Type). Smaller and less robust than *Th. alg. algeriana.* Fastigium of vertex broad, with strongly angulate curved carinae. Elytron short, broad, ratio of length to width 4. Wing short, very broad, external margin very convex, apical lobes broad.

Coloration dark grey, almost black. Elytron without spots. Basal disc of wing intense but not clear rose, with distinct dark fascia and basal ray; apical lobes infumate. In other features not different from typical subspecies.

Length of body 15; pronotum 3·5; elytron 14; hind femur 8·3.

♀ (Paratype). As the male, but larger. Ovipositor more massive. Lower valve with obtuse projection on the external margin.

Length of body 23; pronotum 4·7; elytron 15; hind femur 9·7.

ALGERIA: Chrea, nr. Blida, 1500 m., 26.v.1938, 3 ♂ (including type), 2 ♀ (*B. P. Uvarov*). Aures Mts., 20–21.iv.1937, 1 ♂, 1 ♀ (*A. H. G. Alston*). Aures Mts., Batna to Lambese, vi.1939, 1 ♂ (*M. N. Korsakoff*). Hauts

Plateaux, Trolarel Taza, 1100 m., 25.viii–5.ix.1938, 3 ♂ (*M. A. Volkonsky*). Nr. Adekar, 26.iv.1937, 1 ♂ (*A. H. G. Alston* and *N. D. Simpson*). Djurjura Mts., 29.iv.1937, 1 ♀ (*A. H. G. Alston* and *N. D. Simpson*). Tablat, 900 m., xi.1935, 1 ♀ (*M. N. Korsakoff*). Djebel Adar, Amellal, 1 ♀.

This subspecies occurs on higher mountains (approximately 1500 m.) than the typical subspecies. At lower altitudes *Th. alg. montana* presents a form transitional to neighbouring subspecies.

Thalpomena algeriana **maroccana** subsp. n. (Figs. 18, 32.)

♂ (Type). Larger but less robust than typical subspecies. Fastigium with less curved carinae. Elytron relatively longer, ratio of length to width 4·6. Wing with more broad apical lobes. Hind femur somewhat narrower than in typical subspecies, ratio of length to width 2·8.

Coloration dirty brown. Elytron with small dark spots. Basal disc of wing intense but not clear rose, with dark, broad fascia and broad basal ray; apical lobes obscure.

In other respects as the typical subspecies.

Length of body 18; pronotum 4·1; elytron 16; hind femur 9·8.

♀ (Paratype). As the male, but larger. Ovipositor less slender than in typical subspecies.

Length of body 22; pronotum 5; elytron 18·5; hind femur 11·4.

Spanish Morocco: Xauen Alto, vi.1922, 1 ♂ (type) (*Escalera*). Jebel Dersa, El Haus Jebala, v.1941, 2 ♀ (*E. Morales*). Jebel Mago, El Ajmas Jebala, vi.1930, 1 ♂ (*C. Bolivar*). Tetuan, 1 ♀.

The type is in the Instituto Español de Entomologia; a pair of paratypes in the British Museum.

Thalpomena viridipennis Uvarov. (Figs. 20, 27, 28, 48.)

1927, *Thalpomena algeriana* ab. *viridipennis* Uvarov, *Bull. Soc. Sci. nat. Maroc.* 7 : 207.
1938, *Thalpomena algeriana* ab. *flavipennis* Chapman, *Proc. R. ent. Soc. Lond.* (B) 7 : 100.

♂ (Paratype). Frontal ridge weakly constricted below the ocellus, feebly narrowed at the apex. Fastigium of vertex broad with roundly curved carinae. Pronotum long, above flat; lateral margins straight, little divergent (almost parallel). Median carina strongly convex in front of the first sulcus, straight in the rest. Posterior angle of metazona acute. Metazona twice as long as prozona. Lower margin of lateral lobe sinuate. Elytron broad, ratio of length to width 4·3. Membrane hard, non-transparent. Wing short, broad, external margin strongly convex. Hind femur broad, ratio of length to width 3·1. Hind knee short, broad; upper lobe feebly elongate. Subgenital plate subconical, in profile concave behind, obtuse at the apex.

Coloration dark brownish grey. Elytron without spots. Basal disc of wing bluish green, fascia dark, broad, with a basal ray. Hind femur black inside, with pale fascia in front of the knee; above with two indistinct dark fasciae.

Length of body 16; pronotum 4; elytron 15; hind femur 9·1.

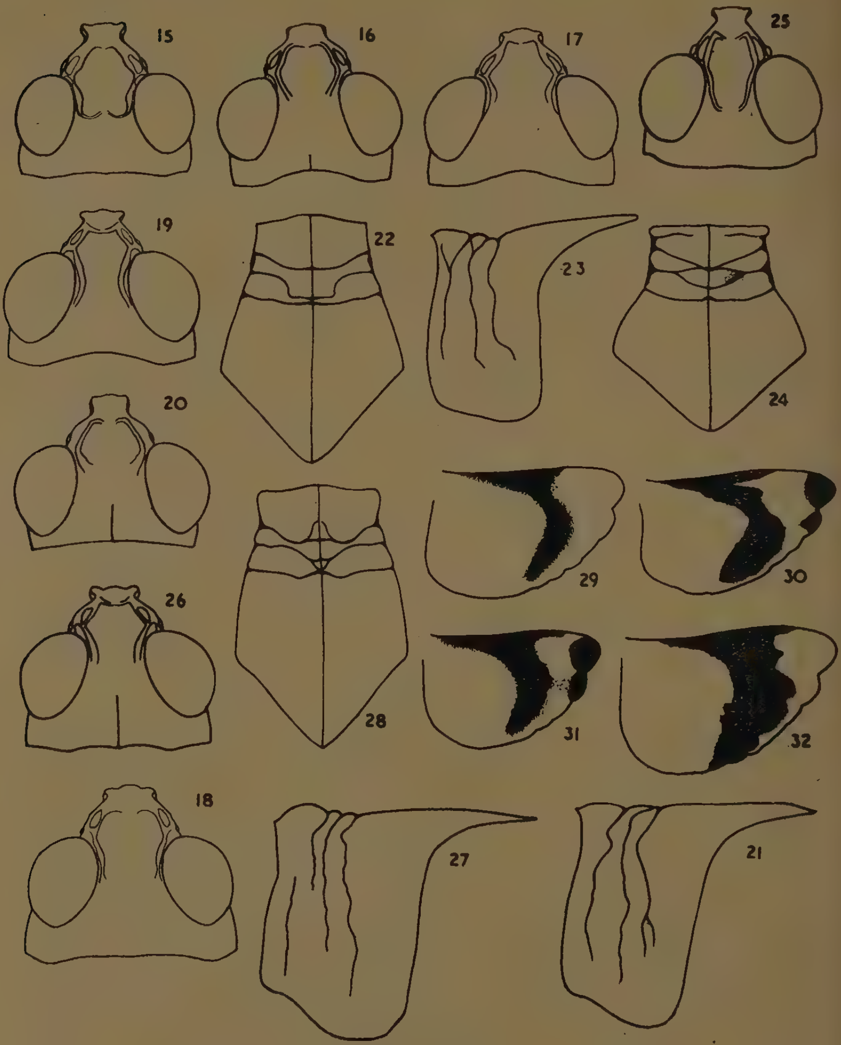
Morocco: Fez, Djebel Zalagh, 25.iii.1923 (*Schulthess*).

♀ (Type). As the male, but larger. Ovipositor short, more robust than in other species; lower valve with rounded projection on the external side.

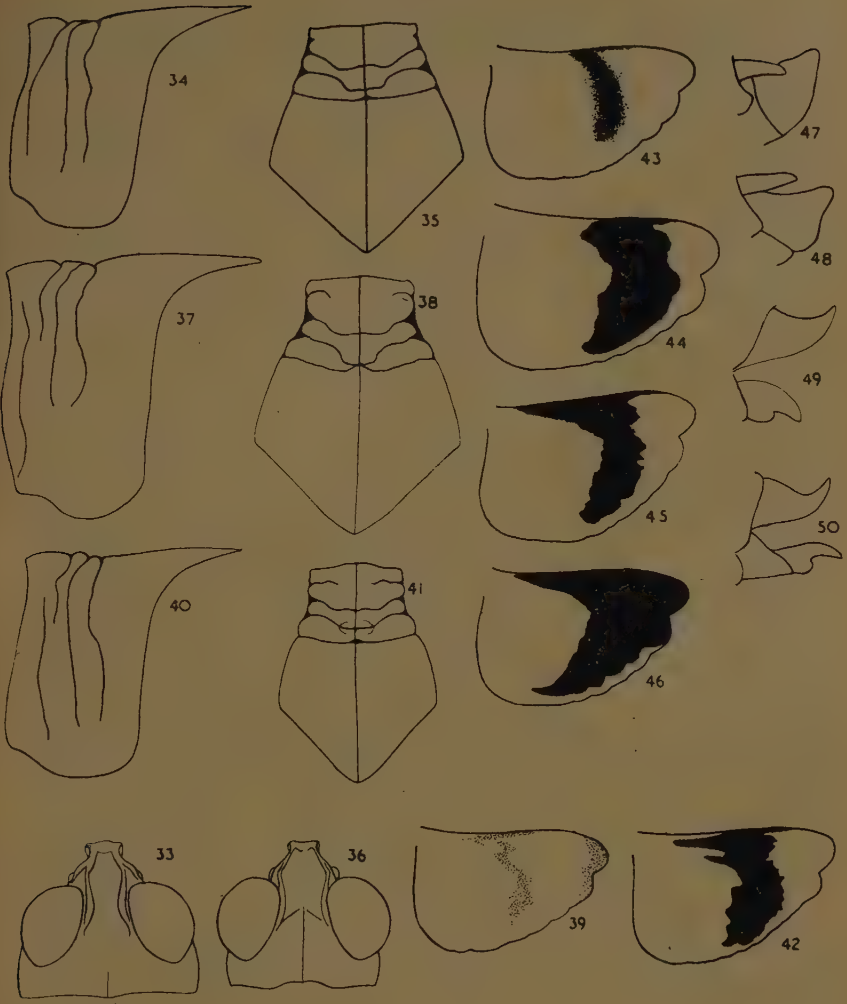
Length of body 25; pronotum 5·5; elytron 20; hind femur 12.

Morocco: Azrou (*Alluaud*).

This species differs sharply from others in the median carina, which is strongly convex in front of the first sulcus.



Figs. 15–32.—(15–20) Head: (15) *Thalpomena algeriana algeriana* (Lucas); (16) *T. algeriana intermedia* subsp. n.; (17) *T. algeriana montana* subsp. n.; (18) *T. algeriana maroccana* subsp. n.; (19) *T. rungsi* sp. n.; (20) *T. viridipennis* Uv. (21) *T. algeriana algeriana* (Lucas). Pronotum in profile. (22) Ditto. Pronotum above. (23) *Thalpomena coerulescens* Uv. Pronotum in profile. (24) Ditto. Pronotum above. (25) *Thalpomena azureipennis* Uv. Head above. (26) *T. coeruleipennis* Finot. Head above. (27) *T. viridipennis* Uv. Pronotum in profile. (28) Ditto. Pronotum above. (29–32) Wing: (29) *Thalpomena algeriana algeriana* (Lucas); (30) *T. algeriana intermedia* subsp. n. (31) *T. algeriana montana* subsp. n.; (32) *T. algeriana maroccana* subsp. n.



FIGS. 33–50.—(33) *Thalpomena deserta* sp. n. Head above. (34) *T. azureipennis* Uv. Pronotum in profile. (35) Ditto. Pronotum above. (36) *Thalpomena coerulescens* Uv. Head above. (37) *T. coeruleipennis* Finot. Pronotum in profile. (38) Ditto. Pronotum above. (39) *Thalpomena deserta* sp. n. Wing. (40) Ditto. Pronotum in profile. (41) Ditto. Pronotum above. (42) *T. coeruleipennis* Finot. Wing. (43) *T. rungsi* sp. n. Wing. (44) *T. viridipennis* Uv. f. *viridipennis*. Wing. (45) *T. viridipennis* f. *fasciata*. Wing. (46) *T. viridipennis* f. *nigra*. Wing. (47) *T. algeriana algeriana* (Lucas). ♂. Subgenital plate. (48) *T. viridipennis* Uv. Ditto. (49) *T. algeriana algeriana* (Lucas). Ovipositor. (50) *T. deserta* sp. n. Ditto.

On wing coloration and the form of fascia *Th. viridipennis* can be divided into five forms. The taxonomic significance of these forms is not yet clear, and possibly they will be considered as separate subspecies when their distribution is better known.

1. Forma *viridipennis.* (Fig. 44.) Fascia broad, scarcely reaching hind margin of wing, without basal ray or with a weak projection instead of the ray. Basal disc of wing light greenish, sometimes with yellowish tinge. (The type of the species belongs to this form.)

Morocco: Middle Atlas Mts. Azrou, 4400 ft., vi.1936, 1 ♀ (*K. H. Chapman* and *G. A. Bisset*). Middle Atlas, Timadit, v.1925, 1 ♂, 2 ♀ (*Escalera*). Chella, xi, 1 ♀ (*Manée M.*).

2. Forma *fasciata.* (Fig. 45.) Wing fascia broad, scarcely reaching hind margin, with distinct, strong basal ray. Basal disc of wing greenish, of more intensive tint than of the first form. (The paratype ♂ belongs to this form.)

Morocco: Middle Atlas, Aguelman Sidi Ali ou Mohammed, 6500 ft., vi.1936, 1 ♀ (*K. H. Chapman* and *G. A. Bisset*). Fez, Djebel Zalagh, 25.iii.1923, 2 ♂ (*Schulthess*). Spanish Morocco: Xauen Alto, v.1922, 3 ♂, 5 ♀ (*Escalera*). Xauen, El Ajmas Jebala, 9–13.v.1932, 1 ♂, 3 ♀ (*Escalera*). Zoumi, 24.ix.1931, 1 ♀. Jebel Dersa, El Hous Jebala, v.1941, 2 ♂, 2 ♀ (*E. Morales*). Lechab, v.1941, 2 ♀ (*E. Morales*). Jebel Mago, El Ajmas Jbala, vi.1930, 1 ♂, 1 ♀ (*C. Bolivar*). H. Kasdir, vi.1941, 1 ♀ (*E. Morales*). Zoco Tlata, Ketama, Rif, vi.1930, 1 ♀ (*C. Bolivar*). Bab Ruadi, Beni Siyyel, vi.1932, 2 ♂, 1 ♀ (*C. Bolivar*). Uad Lau, Beni Hassan Jebala, viii.1938, 1 ♀ (*Escalera*). Bab Hoanas, B. Seyel-Gomare, vii.1941, 1 ♀ (*E. Morales*).

3. Forma *nigra.* (Fig. 46.) Fascia reaching to the hind margin of wing and occupying the whole outer part and apical lobes of the wing. Basal disc of wing light bluish-greenish.

Morocco: Middle Atlas Mts., Azrou, 4400 ft., vi.1936, 2 ♂ (*K. H. Chapman* and *G. A. Bisset*). Middle Atlas, Aguelman Sidi Ali ou Mohammed, 6500 ft., vi.1936, 1 ♂ (*K. H. Chapman* and *G. A. Bisset*). Lechab, v.1941, 2 ♂, 1 ♀ (*E. Morales*). Tizi Taka, Beni Seddat, Rif., v.1920, 2 ♂, 1 ♀ (*C. Bolivar*).

4. Forma *angusta.* Fascia of wing as in f. *fasciata*, but rather narrow (in male diffuse). Basal disc of wing bluish. Veins of wing dark (this character is not found in other forms).

Morocco: Melilla, xii.1941, 1 ♀ (*A. Padro*). Ixmoart, Beni Sicar, Melilla, 1 ♂, 1 ♀ (*A. Padro*).

5. Forma *flavipennis.* Fascia of wing as in f. *fasciata.* Basal disc of wing ochraceous. General coloration pale. (To this form belongs ab. *flavipennis* described by Chapman.)

Morocco: Ifrane, 26.ix.1936, 1 ♀ (*K. H. Chapman*). Beni Ahmed, 1 ♀.

Between f. *nigra* and f. *fasciata* there are transitions which the other forms do not present.

Thalpomena azureipennis Uvarov. (Figs. 25, 34, 35.)

1927, *Thalpomena algeriana* ab. *azureipennis* Uvarov, *Bull. Soc. Sci. nat. Maroc.* **7** : 207.

♂ (Paratype). Frontal ridge weakly concave below the ocellus. Fastigium of vertex narrow, with weakly curved carinae. Pronotum flat above; lateral margins straight, divergent, in prozona, between sulci, scarcely gibbose. Median carina in profile almost straight, scarcely convex in the front of the first sulcus. Metazona 2·1 times as long as prozona, posterior angle right. Lower margin of lateral lobe sinuate. Elytron broad, ratio of length to width 4·7. Wing broad, external margin convex. Hind femur broad, ratio of length to width 3·1. Hind knee broad, with short upper lobe. Subgenital plate short, apex obtuse and slightly recurved.

Coloration grey brownish. Elytron without spots. Basal disc of wing azure blue, with short diffuse fascia, without ray, apex slightly infumate. Hind femur inside dark with two pale fasciae, basal one indistinct, the second, in front of the knee, sharp; above and outside with two indistinct dark fasciae; inside of knee dark. Hind tibia above greyish yellow with dark indistinct ring in the middle nearer to base.

Length of body 17; pronotum 4; elytron 16; hind femur 9.

♀ (Type). As the male, but larger. Carinae of fastigium less sharp. Ovipositor short, valvae weakly incurved; lower valva with rounded projection on the external side.

Length of body 25; pronotum 5·1; elytron 21; hind femur 11·5.

MOROCCO: Grand Atlas, Hte. Reraya (*Alluaud*), 1 ♂, 1 ♀ (type). Upper Reraya, 24.vi.1930, 1 ♂.

Thalpomena coeruleipennis Finot. (Figs. 26, 37, 38, 42.)

1895, *Thalpomena algeriana* var. *coeruleipennis*, Finot, *Ann. Soc. ent. Fr.* **64**: 451.

♀ (Cotype). More slender and smaller than *Th. algeriana.* Frontal ridge constricted below the ocellus, considerably narrowed to the apex. Fastigium short, broad with sharply angulate curved carinae. Pronotum long; lateral margins in prozona between sulci slightly gibbose and rugulose; metazona flat, its lateral margins scarcely convex. Median carina in profile almost straight. Metazona 1·9 times as long as prozona; posterior angle right, its apex acute. Lower margin of lateral lobe strongly sinuate. Elytron relatively narrow, ratio of length to width 4·9. Membrane semi-transparent, coloured. Wing not very broad. Hind femur relatively narrow, ratio of length to width 3·2. Hind knee slender, upper lobe elongate. Ovipositor short, valvae fine, strongly curved; lower valva with small projection on the external side.

Coloration brown. Elytron with the small, indistinct, dark spots. Basal disc of wing hyaline bluish with greenish tint; fascia dark, infumate, with basal ray; apical lobes not infumate. Hind femur inside black, with pale fascia in front of the knee; above with two indistinct dark fasciae. Hind tibia brown, with two light rings.

Length of body 19; pronotum 4; elytron 17; hind femur 11.

ALGERIA: Tlemcen, 15.iv.1880, 2 ♀ (Coll. Finot).

The two females are from Finot's original series in the Paris Museum.

Thalpomena deserta sp. n. (Figs. 39, 40, 41, 50.)

♂ (Type). Less robust than other species of the genus. Frontal ridge constricted below the ocellus, considerably narrowed to the apex. Fastigium long, narrow, with weakly curved carinae. Pronotum above flat; median carina almost straight, in profile slightly raised between second and third sulci; lateral margins in prozona between sulci slightly gibbose, in metazona convex and divergent, metazona 1·9 times as long as prozona, posterior angle right, its apex obtuse. Lower margin of lateral lobe sinuate. Elytron relatively narrow, ratio of length to width 4·6. Reticulation of membrane less dense than in other species. Wing short, external margin less convex than in other species, apical lobe relatively narrow. Hind femur comparatively narrow, ratio of length to width 3·4. Hind knee short, not broad, upper lobe slightly elongate. Subgenital plate short, subconical, apex obtuse.

Coloration pale dirty yellow. Elytron with scattered small dark spots. Wing light rose at the base with indistinct infumate fascia and basal ray. Hind femur inside black with pale fascia in front of the knee; above with two indistinct dark fasciae. Hind tibia dirty yellow with dark rings on the middle and at the apex.

Lower surface of the body with dense long pilosity.

Length of body 17; pronotum 3·5; elytron 16; hind femur 9·7.

♀ (Paratype). Like the male but larger. Ovipositor very short and slender. Lower valva with rounded tooth on the external side.

Length of body 23; pronotum 4·6; elytron 21; hind femur 11·6.

ALGERIA: Djelfa, 3–10.x.1938, 19 ♂ (including type), 22 ♀ (*M. N. Korsakoff*).

The wing fascia has a tendency to disappear and there are specimens without a fascia.

Thalpomena rungsi sp. n. (Figs. 19, 43.)

♂ (Type). Frontal ridge slightly constricted below the ocellus, narrowed to the apex. Fastigium long, widened at the apex; carinae at the apex curved. Pronotum flat; median carina in profile almost straight, slightly raised between second and third sulci; lateral margin of prozona between sulci slightly gibbose; metazona twice as long as prozona, its lateral margins straight, divergent, posterior angle right, its apex acute; lower margin of lateral lobe slightly sinuate. Elytron long, ratio of length to width 4·7. Hind femur relatively long, ratio of length to width 3·3.

Coloration blackish dark grey; elytron without spots; basal disc of wing rose, slightly matt, with dark fascia without basal ray, narrow stripe on the basal part of wing along anterior margin hyaline blue. Hind femur inside black with light fascia in front of the knee. Hind tibia bluish.

Length of body 18·5; pronotum 4; elytron 16·5; hind femur 9·9.

♀ (Paratype). Like the male, but larger. Ovipositor as in *Th. deserta*, but more robust.

Length of body 22·5; pronotum 4·8; elytron 20; hind femur 11·6.

MOROCCO: Gr. Atlas, Taddert, 10.vi.1934, 1 ♂ (type), 1 ♀ (*C. Rungs*). 13.vi.1942, 1 ♀ (*E. Morales*). Gr. Atlas, Tizi Tichka, 2000 m. 12.vi.1942, 1 ♀ (*E. Morales*).

Thalpomena coerulescens Uvarov. (Figs. 23, 24, 36.)

1923, *Thalpomena coerulescens* Uvarov, *Novit. Zool.* 30 : 65.

♂. Small, slender. Frontal ridge feebly constricted below the ocellus, narrowed at the apex. Fastigium narrow, with weakly curved carinae. Pronotum short; median carina in profile slightly concave; lateral margin of prozona between sulci gibbose; metazona 1·5 times as long as prozona, its lateral margins convex and strongly divergent; posterior angle obtuse, its apex rounded; lower margin of lateral lobe almost straight. Elytron long, narrow, ratio of length to width 5·1; apical third subpellucid with reticulation as in *Th. deserta*. Wing rather more elongate than in other species, with less convex external margin. Hind femur relatively narrow, ratio of length to width 3·4. Hind knee narrow, upper lobe elongate. Subgenital plate short, subconical, obtuse at the apex. Body with long pilosity.

Coloration yellowish grey; elytron with small, indistinct, scattered spots. Basal disc of wing pellucid light blue, without fascia. Hind femur inside black with pale fascia in front of the knee; above with two indistinct dark fasciae. Hind tibia dirty yellow with indistinct dark ring between base and middle.

Length of body 16·5; pronotum 3·2; elytron 17; hind femur 8·3.

♀ (Type). As the male, but larger. Ovipositor short, valvae strongly curved; lower valva with tooth on the external side.

Length of body 23; pronotum 4·2; elytron 20; hind femur 10·1.

ALGERIA: Djelfa, 3–4.x.1937, 4 ♂ (including ♂ on which the re-description is based), 2 ♀. Bou-Saada, 6–10.x.1937, 6 ♂, 6 ♀ (*M. N. Korsakoff*). South Oran, Ain Sefra, 1–18.v.1913, 1 ♀ (type).

MOROCCO: Grand Atlas, Ais el Hadj, 1 ♂, 1 ♀. Marrakech, 1 ♀. Taghjicht, Draatrane, 5.iv.1942, 1 ♂, 1 ♀ (*E. Morales*). Gr. Atlas, Tizi N'test, 2100 m. 31.iii.1942, 2 ♂, 1 ♀. Larache, 1 ♂, 1 ♀ (*Escalera*). Tiznit, 21.vi.1943, 1 ♀. El Aioum Du Draa, 6.vi.1942, 2 ♂ (*E. Morales*). Ifni, Zoco Tlata Sboya, 20.x.1941, 1 ♀ (*E. Morales*). Saharlen, el Aioun, Draa, 8.ix.1941, 1 ♀.

TUNISIA: Maknassy, 1 ♂, 2 ♀, 1929 (*C. Dumont*).

Pseudoceles I. Bolivar. (Figs. 2, 6, 9, 13.)

1889, *Pseudoceles* I. Bolivar, *Ann. Soc. ent. Belg.* **43**: 593.
1887, *Thalpomena* Saussure (*partim*), *Mém. Soc. Genève.* **28**: 184.
1930, *Thalpomena* Uvarov, *Eos* **6**: 370.

Type. *Pseudoceles oedipodioides* I. Bol., 1889.

Of medium size, more slender than *Thalpomena*. Head in profile projects above pronotum. Frons oblique, straight. Frontal ridge slightly concave at the ocellus, with a weak constriction or without one; at the apex feebly narrowed. Foveole of vertex concave or flat, irregularly triangular. Fastigium of vertex elongate, with sharp lateral carinae. Pronotum in prozona subcylindrical with slight constriction, in metazona flat or convex; lateral margins divergent, in prozona between sulci gibbose, median carina thin, in profile straight or feebly concave, interrupted by two sulci; posterior angle of metazona right or obtuse. Elytron long, ratio of length to width 4·5–5; apex rounded. Vena intercalata distinct, straight, parallel to the radialis posterior. Wing with feebly convex external margin; basal disc coloured usually with a dark fascia. Hind femur moderately long, not broad. Subgenital plate of male short, subconical, apex obtuse. Ovipositor short, slender, valvae incurved; lower valva with a projection on the external margin.

Uvarov (1930) has synonymized *Pseudoceles* with *Thalpomena*, obviously because the latter genus has been too widely interpreted, and I consider it necessary to restore it for a number of Western Asiatic species which form a group quite distinct from the true *Thalpomena* of N.W. Africa.

Key to species of *Pseudoceles*.

1 (2). Metazona of pronotum in profile strongly convex; posterior angle right, with acute apex (figs. 75, 90) . . . . **uvarovi** sp. n.
2 (1). Metazona of pronotum in profile straight or slightly convex; posterior angle right or obtuse.
3 (6). Basal disc of wing yellow.
4 (5). Fastigium of vertex regularly oval; its carinae convergent at apex and at base (fig. 82). Prozona of pronotum smooth, weakly gibbose between sulci on the lateral margin (fig. 81) **turcicus** sp. n.
5 (4). Fastigium widened to apex; its carinae divergent to apex and to base (fig. 74). Lateral margin of prozona between sulci strongly gibbose and rugulose (fig. 78) . . . *ledereri* (Saussure).

6 (3). Basal disc of wing not yellow.

7 (12). Hind tibia rose above. Basal disc of wing light rose.

8 (9). Fastigium almost regularly oval (fig. 53). Prozona of the pronotum considerably narrower than metazona, posterior angle of metazona acute (fig. 58). Anterior margin of lateral lobe of pronotum straight (fig. 92). . . . . . **palaestinus** sp. n.

9 (8). Fastigium narrowed to the apex, its carinae irregularly curved (figs. 55, 61). Anterior angle of pronotum in profile acute, strongly projecting forwards (figs. 84, 87); prozona rather narrower than metazona (figs. 60, 66); posterior angle of metazona obtuse.

10 (11). Lateral margin of prozona between sulci slightly gibbose; in metazona strongly divergent, straight (fig. 60). Width of lateral lobe of pronotum almost equal to its height (fig. 87) **zangezuri** sp. n.

11 (10). Lateral margin of prozona between sulci strongly gibbose and rugulose; in metazona weakly divergent, convex (fig. 66). Height of lateral lobe of pronotum 1·5 times the width (fig. 84) **armeniacus** sp. n.

12 (7). Hind tibia bluish.

13 (14). Metazona of pronotum more than twice as long as prozona (fig. 70); lateral margins of metazona strongly divergent; anterior margin of lateral lobe with projection on the middle (fig. 85) *violaceus* (Moritz).

14 (13). Metazona of pronotum less than twice as long as prozona; its lateral margins moderately divergent; anterior margin of lateral lobe straight or weakly sinuate, without projection (figs. 96, 97).

15 (16). Fastigium of vertex considerably broader at the apex than at the base (fig. 72) . . . . **arpatchai** sp. n.

16 (15). The apex of fastigium as broad as the base or narrower (fig. 64, 51, 52).

17 (18). Posterior angle of pronotum acute, with acute apex (fig. 69); lower margin of lateral lobe almost straight (fig. 97) . **tari** sp. n.

18 (17). Posterior angle of pronotum right or obtuse, with the apex rounded or obtuse (figs, 56; 68).

19 (20). Height of lateral lobe of pronotum more than 1·5 times its length (fig. 86) . . . . *persa* (Saussure).

20 (19). Height of lateral lobe of pronotum little more than or equal to its length (figs. 91, 93, 98).

21 (24). Posterior angle of metazona of pronotum with rounded apex (figs. 68, 77).

22 (23). Fastigium of vertex 2·5 times as long as broad (fig. 63). Metazonal process, in profile, very short (fig. 91); lateral margin of metazona convex (fig. 68) . . . . **demavendi** sp. n.

23 (22). Fastigium 1·5 times as long as broad (fig. 73). Metazonal process, in profile, short (fig. 98); lateral margin of metazona straight (fig. 77) . . . . **elbursi** sp. n.

24 (21). Posterior angle of metazona with obtuse apex (57, 59, 79).

25 (26). Basal disc of wing intensive red . . . . *obscurus* (Uvarov).

26 (25). Basal disc of wing rose or blue.

27 (28). Fastigium oval (fig. 54). Basal disc of wing rose *oedipodioides* I. Bolivar.

28 (27). Fastigium with irregularly curved carinae (figs. 52, 62). Basal disc of wing bluish or indigo bluish.
29 (30). Carinae of fastigium curved in their whole length (fig. 52). Pronotum more slender (fig. 89) . . . . **ebneri** sp. n.
30 (29). Carinae of fastigium in middle part straight (fig. 62). Pronotum less slender (fig. 88) . . . . **popovi** sp. n.

Pseudoceles persa (Saussure). (Figs. 51, 56, 86.)

1884, *Thalpomena persa* Saussure, *Mém. Soc. Genève*, **28** : 184.

♂. Frontal ridge slightly constricted below the ocellus, at the apex narrowed. Fastigium of vertex elongate, narrowed at the apex, with angulate curved carinae. Pronotum long; median carina in profile almost straight; lateral margin of prozona between sulci gibbose; metazona flat, 2·2 times as long as prozona, its lateral margins convex, posterior angle right, its apex obtuse; lower margin of lateral lobe strongly sinuated. Elytron long and broad, ratio of length to width 4·5; membrane thin, subpellucid, coloured. Wing long and broad, with external margin more convex than in the other species. Hind femur long, ratio of length to width 3·5. Hind knee with elongated upper lobe and deep excision. Subgenital plate short, subconical, obtuse.

Coloration light brownish yellow; elytron without spots; basal disc of wing light rose, fascia indistinct, infumate, apex slightly infumate. Hind femur inside black with pale fascia in front of the knee; above and below with two indistinct dark fasciae, disappearing outside; knee light brown. Hind tibia dirty blue with yellowish ring at the base.

Length of body 18; pronotum 4; elytron 18; hind femur 10.

♀. As the male but larger. Carinae of fastigium less sharp. Ovipositor with strongly curved valvae; lower valva with large, rounded projection.

Length of body 27; pronotum 6; elytron 23; hind femur 13·5.

PERSIA: Elburs, Schahkuh, 1 ♂, 1 ♀ (Coll. Brunner v. Wattenwyl).

The data on the label of the male specimen described are the same as those given by Saussure in his work. Probably it is the type of this species, or at least one of cotypes.

By its broad elytra and wings, *P. persa* differs strongly from other species of *Pseudoceles* and may represent another genus.

Pseudoceles ebneri sp. n. (Figs. 52, 57, 89.)

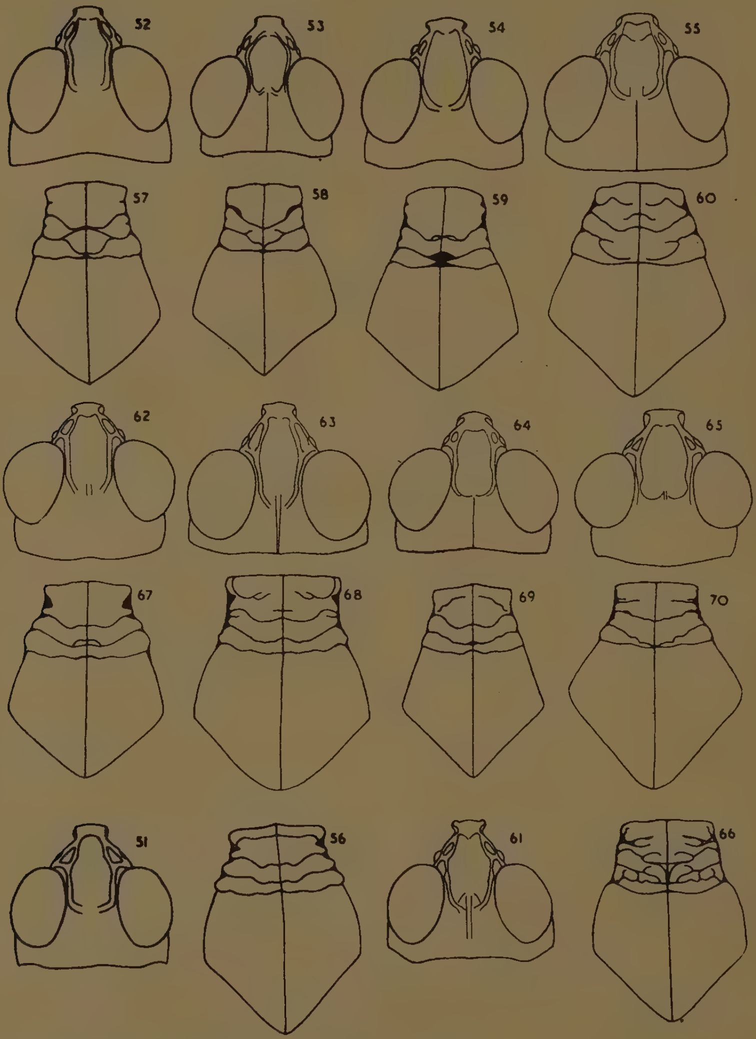
♂ (Type). Frontal ridge concave at the ocellus, slightly constricted below it and weakly narrowed at the apex. Fastigium of vertex long, strongly concave, with sharply angulate carinae. Pronotum long, narrow; median carina in profile straight; lateral margin of prozona, between sulci, gibbose; metazona flat, twice as long as prozona, its lateral margins straight, feebly divergent, posterior angle right, its margins slightly convex. Lower margin of lateral lobe sinuate. Elytron long, not broad, ratio of length to width 4·7. Wing relatively long, with feebly convex external margin. Hind femur long, ratio of length to width 3·5. Hind knee with little elongate upper lobe and broad excision. Subgenital plate short, subconical, obtuse at the apex.

Coloration dark brown; elytron without spots; basal disc of wing indigo blue, fascia indistinct with basal ray, apex infumate. Hind femur inside black with light distinct fascia in front of the knee; above and outside with two indistinct dark fasciae. Hind tibia above indigo-bluish with indistinct dark ring between base and middle. Abdomen above and below, towards apex, with indigo-blue stripe.

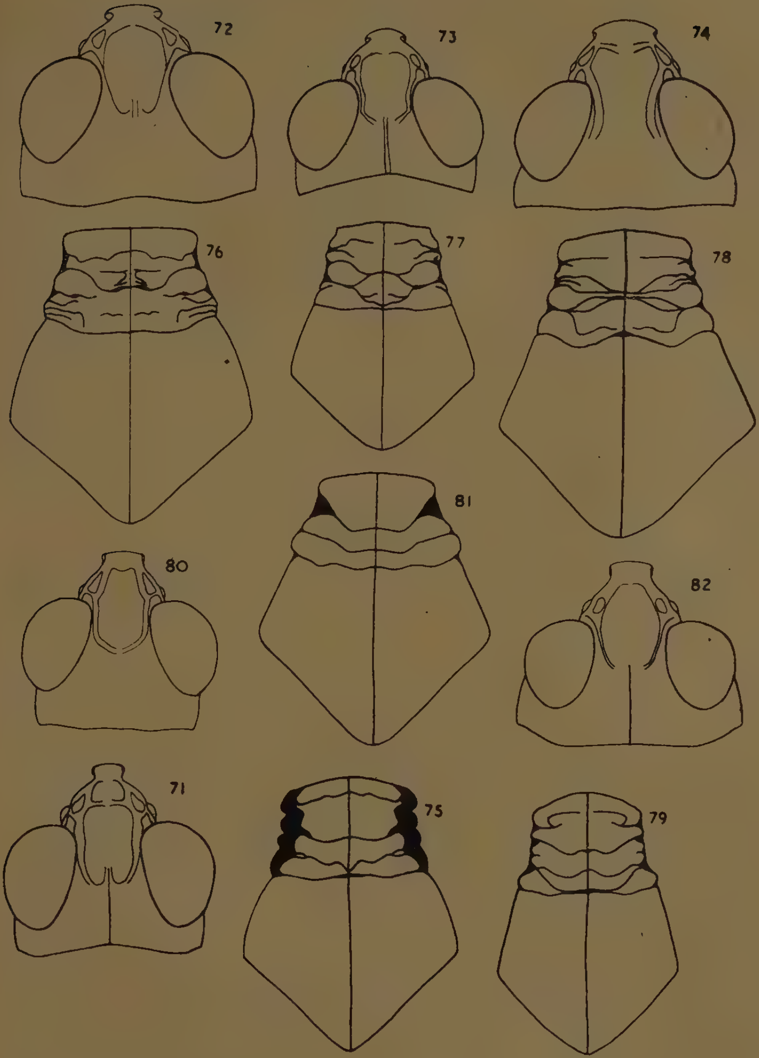
Length of body 17; pronotum 4; elytron 19; hind femur 11·7.

♀ (Paratype). As the male, but larger. Ovipositor short, valvae feebly curved; lower valva with rounded projection on the external margin.

Length of body 24; pronotum 5; elytron 23; hind femur 12·7.



FIGS. 51–70.—(51–55) Head above : (51) *Pseudoceles persa* (Sauss.) ; (52) *P. ebneri* sp. n. ; (53) *P. palaestinus* sp. n. ; (54) *P. oedipodioides* I. Bol. ; (55) *P. zangezuri* sp. n. (56–60) Pronotum above : (56) *Pseudoceles persa* (Sauss.) ; (57) *P. ebneri* sp. n. ; (58) *P. palaestinus* sp. n. ; (59) *P. oedipodioides* I. Bol. ; (60) *P. zangezuri* sp. n. (61–65) Head above : (61) *Pseudoceles armeniacus* sp. n. ; (62) *P. popovi* sp. n. ; (63) *P. demavendi* sp. n. ; (64) *P. tari* sp. n. ; (65) *P. violaceus* (Moritz). (66–70) Pronotum above : (66) *Pseudoceles armeniacus* sp. n. ; (67) *P. popovi* sp. n. ; (68) *P. demavendi* sp. n. ; (69) *P. tari* sp. n. ; (70) *P. violaceus* (Moritz).



Figs. 71–82.—(71–74) Head above: (71) *Pseudoceles uvarovi* sp. n.; (72) *P. arpatchai* sp. n.; (73) *P. elbursi* sp. n.; (74) *P. ledereri* (Sauss.). (75–79) Pronotum above: (75) *Pseudoceles uvarovi* sp. n.; (76) *P. arpatchai* sp. n.; (77) *P. elbursi* sp. n.; (78) *P. ledereri* (Sauss.); (79) *P. obscurus* (Uv.). (80) *P. obscurus* (Uv.). Head above. (81) *P. turcicus* sp. n. Pronotum above. (82) Ditto. Head above.

SYRIA: Lebanon; Besharra-Baalbec Pass, 8750 ft., 20.viii.1944, 6 ♂ (including type), 4 ♀. Quadishab, 6000 ft., 20.viii.1944, 1 ♀ (*H. B. Cott*). Baalbec, 29.vii.1928, 2 ♂, 2 ♀. Djebel Sannin, 16.vii.1928, 1 ♂. Bscharre, Zederwald, 2050 m., 10.viii.1928, 2 ♂, 2 ♀ (*R. Ebner*).

Some paratypes are in the collection of Prof. R. Ebner in Vienna.

Pseudoceles palaestinus sp. n. (Figs. 53, 58, 92.)

♂ (Type). Frontal ridge strongly concave below the ocellus, almost without constriction. Fastigium of vertex strongly concave, oval. Pronotum long; median carina in profile almost straight; lateral margin of prozona between sulci feebly gibbose; metazona flat, 1·8 times as long as prozona, its lateral margins strongly divergent, slightly convex, posterior angle right, with acute apex and with slightly concave lateral sides; lower margin of lateral lobe scarcely sinuate, almost straight. Elytron relatively long, ratio of length to width 5; membrane subpellucid, coloured. Wing long, with weakly convex external margin. Hind femur relatively short, ratio of length to width 3·3. Upper lobe of the hind knee feebly elongate, excision narrow. Subgenital plate short, subconical, slightly concave behind.

Coloration dark brown; elytron without spots; basal disc of wing light rose, pellucid, with indistinct infumate fascia and basal ray; apex slightly infumate. Hind femur inside dark, in front of the knee with pale fascia; above and outside with two indistinct dark fasciae; hind knee brownish; hind tibia above rose. Abdomen above towards apex with a longitudinal rose stripe.

Length of body 17; pronotum 3·7; elytron 17·7; hind femur 10.

PALESTINE: Djebel Matrate to Wadi-d-Tawil, 1 ♂ (type) (*F. S. Bodenheimer*).

Pseudoceles oedipodioides I. Bolivar. (Figs. 54, 59, 95.)

1899, *Pseudoceles oedipodioides* I. Bolivar, *Ann. Soc. ent. Belg.* **43**: 593.
1930, *Thalpomena ledereri* Uvarov (*nec* Saussure), *Eos* **6**: 370.

♂. Frontal ridge without constriction, at apex narrower. Fastigium of vertex strongly concave, its carinae arcuate. Pronotum relatively long; median carina in profile almost straight; lateral margin of prozona between sulci strongly gibbose and rugulose; metazona 1·6 times as long as prozona, smooth, its lateral margins moderately divergent, slightly convex; posterior angle obtuse; lower margin of lateral lobe strongly sinuate. Elytron narrow, obliquely truncate at the apex, ratio of length to width 4·9. Wing relatively narrow, external margin feebly convex. Hind femur relatively long, ratio of length to width 3·4. Upper lobe of the hind knee elongate, excision shallow. Subgenital plate short, subconical, obtuse at the apex.

Coloration brownish grey; elytron with dark, indistinct, scattered spots; basal disc of wing dark rose, semi-transparent, fascia infumate, diffuse, with basal ray; apex slightly infumate. Hind femur inside black with pale fascia in front of the knee; above and outside with two dark indistinct fasciae; hind knee inside black; hind tibia above bluish.

Length of body 18; pronotum 3·9; elytron 17; hind femur 10.

TURKEY: Kurdistan, Nimrud (38° 39′ N., 42° 10′ E.), 1908, 1 ♂ (*F. Oswald*).

Pseudoceles oedipodioides was described by I. Bolivar from a single female from Bimbogha-Dagh (38° 20′ N., 36° 30′ E.). The male is from a locality sufficiently near to the original and its characters agree with Bolivar's description.

Pseudoceles zangezuri sp. n. (Figs. 55, 60, 87.)

♂ (Type). Frontal ridge constricted below the ocellus, narrowed to the apex. Fastigium of vertex long, narrower towards apex, its carinae irregularly curved. Occiput with a carina. Pronotum relatively broad; median carina in profile almost straight; lateral margin of prozona between sulci gibbose; metazona flat, 1·7 times as long as prozona, its lateral margins straight and strongly divergent; posterior angle right, its apex obtuse; lower margin of lateral lobe feebly sinuate. Elytron relatively long, ratio of length to width 4·9. Wing elongate, its external margin slightly concave. Hind femur moderately long, ratio of length to width 3·4. Upper lobe of the hind knee elongate. Subgenital plate short, subconical, obtuse at the apex.

Coloration brownish grey; elytron with dark indistinct spots; basal disc of wing hyaline rose; fascia with basal ray, infumate, indistinct; apex slightly infumate. Hind femur inside dark, with light fascia in front of the knee; above and outside with two indistinct dark fasciae. Hind tibia above rose.

Length of body 18; pronotum 4; elytron 17; hind femur 10·5.

♀ (Paratype). Like the male but larger. Carinae of fastigium less strong. Ovipositor short; lower valva with large obtuse projection on the external side.

Length of body 23; pronotum 5; elytron 21; hind femur 13.

ARMENIA: Zangezur, prov. Megry (39° 0′ N., 46° 0′ E.), 14.vi.1925, 2 ♂ (including type), 1 ♀ (*M. Riabov*).

Pseudoceles armeniacus sp. n. (Figs. 61, 66, 84.)

♂ (Type). Margins of the frontal ridge almost parallel, slightly convergent at the apex. Fastigium of vertex long, narrowed towards apex, its carinae irregularly curved. Pronotum relatively narrow, median carina in profile slightly concave; lateral margin of prozona strongly gibbose and rugulose between sulci; sulci with numerous branches; metazona 1·9 times as long as prozona, its lateral margins strongly convex and feebly divergent; posterior angle right, its apex obtuse; lower margin of the lateral lobe almost straight, its angles broadly rounded. Elytron long, ratio of length to width 4·6. Hind femur moderately long, ratio of length to width 3·2. Upper lobe of the hind knee rather elongate. Subgenital plate short, subconical, obtuse at the apex.

Coloration light brownish grey; elytron with scattered dark spots; basal disc of wing light reddish rose; apex feebly infumate. Hind femur inside dark with light fascia in front of the knee; above and outside with two indistinct dark fasciae. Hind tibia above rose.

Length of body 16; pronotum 4; elytron 16; hind femur 9.

♀ (Paratype). Like the male but larger. Lower valva of ovipositor with large, obtuse, angulate projection on the external margin.

Length of body 21; pronotum 5; elytron 21; hind femur 12.

ARMENIA: Amamly, 20.vii.1925, 3 ♂ (including type), 3 ♀ (*M. Riabov*).

Pseudoceles popovi sp. n. (Figs. 62, 67, 88.)

♂ (Type). Frontal ridge weakly concave and slightly constricted below the ocellus, narrowed towards apex. Fastigium of vertex with feebly curved, in the middle part straight and parallel, carinae, and with a short basal carinula. Pronotum in profile almost straight, slightly raised in prozona in front of the first sulcus; lateral margin of prozona between sulci gibbose; metazona 1·6 times as long as prozona, its lateral margins smooth, straight and moderately divergent; posterior angle right, with obtuse apex; lower margin of lateral lobe moderately sinuate. Elytron long, rounded at the apex, ratio of length to width 4·7. Hind femur moderately long, ratio of length to width 3·2. Hind knee with short, broad upper lobe and weak excision. Subgenital plate short, subconical, obtuse at the apex.

Coloration brownish grey; elytron with diffused small spots. Basal disc of wing light indigo blue, with indistinct infumate fascia and basal ray. Hind femur black inside, with light fascia in front of the knee; above and outside with two indistinct dark fasciae. Hind tibia bluish.

Length of body 18; pronotum 4; elytron 16·5; hind femur 9·5.

♀ (Paratype). Like the male, but larger. Lateral margin of prozona of pronotum between sulci less gibbose. Lower valva of ovipositor with rounded projection on the external margin.

Length of body 26; pronotum 5·3; elytron 21·5; hind femur 13.

PERSIA: Mountains N. of Tehran, 26.vii.1943, ♂ (type), 1 ♀ (*B. P. Uvarov*). Foothills of Elburs, near Tehran, 9.vii.1947, 1 ♂, 2 ♀ (*G. V. Popov*).

Pseudoceles demavendi sp. n. (Figs. 63, 68, 91.)

♂ (Type). Frontal ridge feebly concave and scarcely constricted at ocellus, weakly narrowed towards apex. Fastigium with sharp, feebly curved carinae, with an occipital carinula. Pronotum in profile almost straight; lateral margin of prozona gibbose and rugulose between sulci; metazona 1·7 times as long as prozona, above flat, its lateral margins convex, smooth and moderately divergent; posterior angle obtuse, with rounded apex; lower margin of lateral lobe sinuate. Elytron with slightly broadened anal area; ratio of length to width 4·5. Hind femur relatively long, ratio of length to width 3·3. Hind knee with slightly elongate upper lobe and narrow, shallow excision. Subgenital plate short, subconical.

Coloration brownish grey; elytron with dark scattered spots. Basal disc of wing light reddish with infumate fascia and basal ray; apex infumate. Hind femur inside dark, with light fascia in front of the knee; above and outside with two dark fasciae. Hind tibia bluish.

Length of body 19; pronotum 4; elytron 18; hind femur 10·5.

♀ (Paratype). Like the male but larger. Lateral margin of prozona of pronotum between sulci less gibbose. Lower valva of ovipositor with tooth form projection on the external side.

Length of body 24; pronotum 5·4; elytron 21; hind femur 13.

PERSIA: Elburs, Rehne, 2000 m., 21.vii.1936, 1 ♂ (type). Rehne-Demavend, 2700–3600 m., 21.vii.1936, 3 ♂, 2 ♀ (*R. Ebner*).

Type in the collection of Prof. R. Ebner, Vienna. One pair of paratypes in the British Museum.

Pseudoceles tari sp. n. (Figs. 64, 69, 97.)

♂ (Type). Frontal ridge feebly concave at the ocellus and weakly constricted below it; narrowed towards apex. Fastigium of vertex with weakly curved not sharp carinae and with an occipital carina. Pronotum relatively slender, in profile almost straight; lateral margin of prozona between sulci weakly gibbose; metazona 1·9 times as long as prozona, its lateral margins smooth and straight; posterior angle right, with acute apex; lower margin of lateral lobe weakly sinuate. Elytron with slightly broadened anal area, ratio of length to width 4·2. Hind femur moderately short, ratio of length to width 3·1. Hind knee with short upper lobe and shallow excision. Subgenital plate short, subconical, obtuse at the apex.

Coloration brownish grey; elytron with small, dark spots. Basal disc of wing light indigo blue, with indistinct infumate fascia and basal ray, apex infumate. Hind femur inside dark with light fascia in front of the knee; above and outside with two dark indistinct fasciae. Hind tibia above bluish.

Length of body 16; pronotum 4; elytron 15·5; hind femur 9·5.

♀ (Paratype). Like the male but larger. Lower valva of ovipositor with large projection on the external side.

Length of body 23; pronotum 5; elytron 22; hind femur 12·2.

PERSIA: Elburs, Demavend, Lake Tar, 2200 m., 17.vii.1936, 1 ♂ (type). 2100 m., 14–16.vii.1936, 1 ♂, 3 ♀ (*R. Ebner*).

Type in the collection of Prof. R. Ebner, Vienna; one pair of paratypes in the British Museum.

Two other females have the basal disc of the wing light rose (with slight violet tinge), and may be called f. *roseipennis*. In other respects they do not differ from the typical form.

Pseudoceles violaceus (Moritz). (Figs. 65, 70, 85.)

1928, *Thalpomena persa* ab. *violacea* Moritz, *Askhabad St. Plant Prot.*: 41.
1929, *Thalpomena persa* ab. *violacea* Uvarov and Moritz, *Ann. Mag. nat. Hist.* (10) 4 : 535.

♂ (Paratype). Frontal ridge without concavity, feebly constricted below and widened above the ocellus, weakly narrowed towards apex. Fastigium long, narrowed towards apex, with the carinae sharp and a short basal carinula. Pronotum in prozona constricted, in metazona strongly broadened; median carina in profile slightly raised in prozona and feebly convex in metazona; lateral margin of prozona between sulci gibbose and rugulose; metazona 2·2 times as long as prozona, its lateral margins smooth, straight and strongly divergent; posterior angle right, with obtuse apex; anterior margin of lateral lobe with rounded projection, lower margin sinuate. Elytron narrow, slightly narrower at the apex; ratio of length to width 5·3. Hind femur relatively long, ratio of length to width 3·5. Hind knee with elongated upper lobe and weak excision. Subgenital plate short, subconical, obtuse at the apex.

Coloration light grey; elytron with dark diffused spots. Basal disc of wing light violet, hyaline, with indistinct infumate fascia and basal ray; apex slightly infumate. Hind femur inside black with a sharp light fascia in front of the knee and incomplete fascia in the middle; above with two indistinct dark fasciae. Hind tibia above bluish.

Length of body 17; pronotum 4; elytron 17; hind femur 9.

♀ (Paratype). Like the male, but larger. Lower valva of ovipositor with angulate projection on the external margin.

Length of body 23; pronotum 5·3; elytron 22; hind femur 10.

TRANSCASPIA: Firuza, 25.viii.1927, 1 ♂, 3 ♀.

Pseudoceles uvarovi sp. n. (Figs. 71, 75, 90.)

1911, *Thalpomena ledereri* Ikonnikov (*nec* Saussure), *Rev. russ. Ent.* 11 : 12.

♂ (Type). Frontal ridge scarcely concave and constricted below the ocellus; feebly narrowed towards apex. Fastigium of vertex long, strongly concave, its carinae sharp, sinuate; occiput with median carina. Pronotum relatively robust; median carina, in profile, in prozona straight, in metazona convex; lateral margin of prozona between sulci sharply gibbose and rugulose; metazona twice as long as prozona, its disc strongly convex, lateral margins convex, smooth and strongly divergent; posterior angle right, its apex acute; lower margin of lateral lobe weakly sinuate. Elytron hard, with denser reticulation than in other species; ratio of length to width 4·4. Hind femur moderately long, ratio of length to width 3·3. Upper lobe of the hind knee long, rounded at apex. Subgenital plate narrow, subconical, obtuse at the apex.

Coloration brownish grey; elytron with dark, indistinct, small spots. Basal disc of wing pink, semi-transparent, with broad, dark, distinct fascia and basal ray; apex slightly obscured. Hind femur inside dark, with light fascia in front of the knee; above and outside with two indistinct dark fasciae. Hind knee inside dark. Hind tibia dirty blue, with light ring at the base.

Length of body 19; pronotum 4·8; elytron 19; hind femur 11·5.

♀ (Paratype). Like the male but larger. Ovipositor short; lower valva with strong angulate projection on the external side.

Length of body 25; pronotum 6; elytron 23; hind femur 14.

TRANSCAUCASIA: Georgia, Mzchet (near Tiflis), vi.1910, 2 ♂ (including type), 1 ♀ (*Bankovsky*). 2.vi.1915, 1 ♂ (*B. P. Uvarov*).

This common Transcaucasian species has always been incorrectly recorded in the past as *Th. ledereri* Saussure.

Pseudoceles arpatchai sp. n. (Figs. 72, 76, 96.)

♀ (Type). Frons in profile broadly rounded at the apex. Frontal ridge low; below the ocellus impressed and slightly constricted; above the ocellus slightly widened; narrowed towards apex. Foveolae of vertex flat. Fastigium short, feebly concave, broadened at the apex; carinae obsolescent, oval curved, with short basal carinula. Pronotum relatively broad; median carina weakly concave in profile; lateral margin of prozona between sulci strongly gibbose; metazona flat, 1·9 times as long as prozona, its lateral margins smooth, slightly concave and moderately divergent; posterior angle right, its apex obtuse; lower margin of lateral lobe almost straight, scarcely sinuate. Elytron with stronger projection at the base of anterior margin than in other species. Ratio of length to width 4·7. Hind femur moderately short, ratio of length to width 3·1. Lower valva of ovipositor with strong angular projection on the external margin.

Coloration pale brown, slightly reddish; elytron reddish, with dark diffused spots. Basal disc of wing light rose, hyaline; fascia with basal ray smoky, indistinct. Hind femur inside dark, with two light fasciae. Hind tibia above bluish.

Length of body 23·5; pronotum 5; elytron 21; hind femur 12.

ARMENIA: River Arpatchai, ix.1929, 2 ♀ (including type) (*T. V. Weber*).

Pseudoceles elbursi sp. n. (Figs. 73, 77, 98.)

♂ (Type). Frontal ridge feebly concave and with a slight constriction at the ocellus, narrowed towards apex. Fastigium of vertex broadened to the apex with weakly sinuate carinae, and with an occipital carina. Pronotum relatively slender; median carina in profile straight; lateral margin of prozona between sulci strongly gibbose and rugulose; metazona smooth, 1·8 times as long as prozona, its lateral margins straight, moderately divergent; posterior angle obtuse, short, with rounded apex; lower margin of lateral lobe feebly sinuate. Elytron with slightly broadened anal area; ratio of length to width 4·6. Hind femur moderately long, ratio of length to width 3·4. Hind knee with short upper lobe and weak excision. Subgenital plate short, subconical, strongly obtuse at the apex.

Coloration greyish brown; elytron with small dark spots. Basal disc of wing rose (with purplish tinge), hyaline; infumate fascia and basal ray very indistinct. Hind femur inside dark with a light fascia in front of the knee; above with two indistinct dark fasciae. Hind tibia above bluish.

Length of body 16; pronotum 3·7; elytron 16; hind femur 9·5.

♀ (Paratype). Like the male, but larger. Basal disc of wing more clear rose. Lower valva of ovipositor with large tooth on the external side.

Length of body 21·5; pronotum 5; elytron 21; hind femur 12·2.

PERSIA: Elburs, Kendevan Pass, 3000 m., 3–9.vii.1936, 2 ♂ (including type), 1 ♀ (*R. Ebner*).

Type in the collection of Prof. R. Ebner, Vienna; one male paratype in the British Museum.

Pseudoceles ledereri (Saussure). (Figs. 74, 78, 83.)

1884, *Thalpomena ledereri* Saussure, *Mém. Soc. Genève*, **28** : 184.

♀. Frontal ridge slightly constricted below the ocellus, scarcely narrowed at the apex. Fastigium of vertex long, strongly concave, its carinae curved, divergent towards apex and towards base, and convergent between eyes. Pronotum relatively large, long; median carina in profile almost straight; lateral margin of prozona between sulci sharply gibbose; metazona smooth, its lateral margins straight, strongly divergent; posterior angle obtuse, its apex rounded; lower margin of lateral lobe weakly sinuate. Elytron long, ratio of length to width 4·3; apical part slightly narrowed. Hind femur long, ratio of length to width 3·2. Upper lobe of hind knee slightly elongate with a small excision. Ovipositor short, slender; valvae strongly curved; lower valva with large rounded projection on the external side.

Coloration dirty brown; elytron without spots, membrane light brown; basal disc of wing muddy yellow, with a broad brown fascia and basal ray; apex darkened. Hind femur inside dark, with two pale fasciae; outside and above with one dark fascia. Hind knee dark. Hind tibia above bluish.

Length of body 23; pronotum 5·2; elytron 20; hind femur 12.

TURKEY: Güllele, Taurus, 1 ♀ (Coll. Brunner v. Wattenwyl, *ex* Coll. Lederer).

Pseudoceles turcicus sp. n. (Figs. 81, 82, 94.)

♀ (Type). Frontal ridge scarcely concave below the ocellus, without constriction, scarcely narrowed towards apex. Fastigium of vertex regularly oval, its carinae not strong. Pronotum moderately broad; median carina in profile straight; prozona above smooth, its lateral margin between sulci gibbose; metazona twice as long as prozona, flat, smooth, its lateral margins straight, moderately divergent; posterior angle obtuse, with obtuse apex; lower margin of lateral lobe sinuate. Elytron with slightly broadened anal area; ratio of length to width 4·7. Hind femur relatively short, ratio of length to width 3·1. Upper lobe of the hind knee short, excision shallow. Lower valva of ovipositor with large obtusangulate projection on the external side.

Coloration dirty yellow; elytron with brownish spots. Basal disc of wing yellow, semi-transparent, with broad infumate fascia and basal ray; apex slightly infumate. Hind femur inside dark, with pale fascia in front of the knee; above and outside with dark sharp fascia. Hind tibia above bluish, with dark and light rings in front of the base.

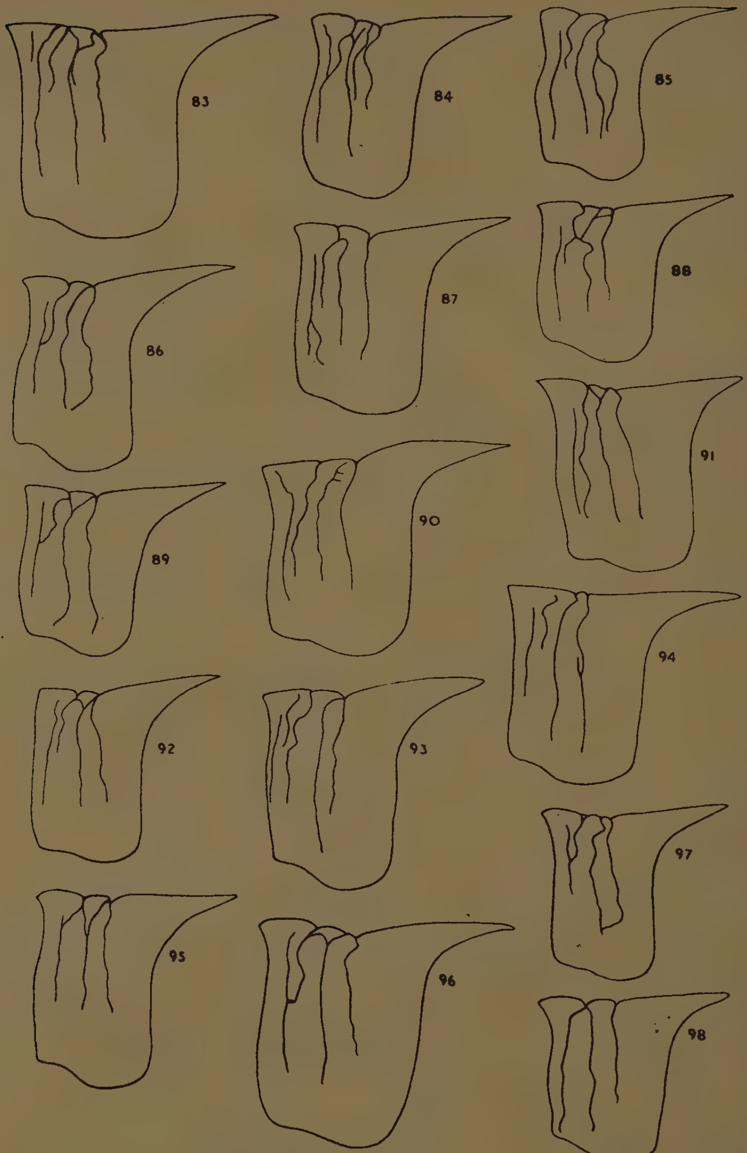
Length of body 20·5; pronotum 4·7; elytron 19; hind femur 10·7.

TURKEY: Vilayet Mughla, Gidder Dagh, 2000 m., 5.viii.1947, 1 ♀ (*P. H. Davis*).

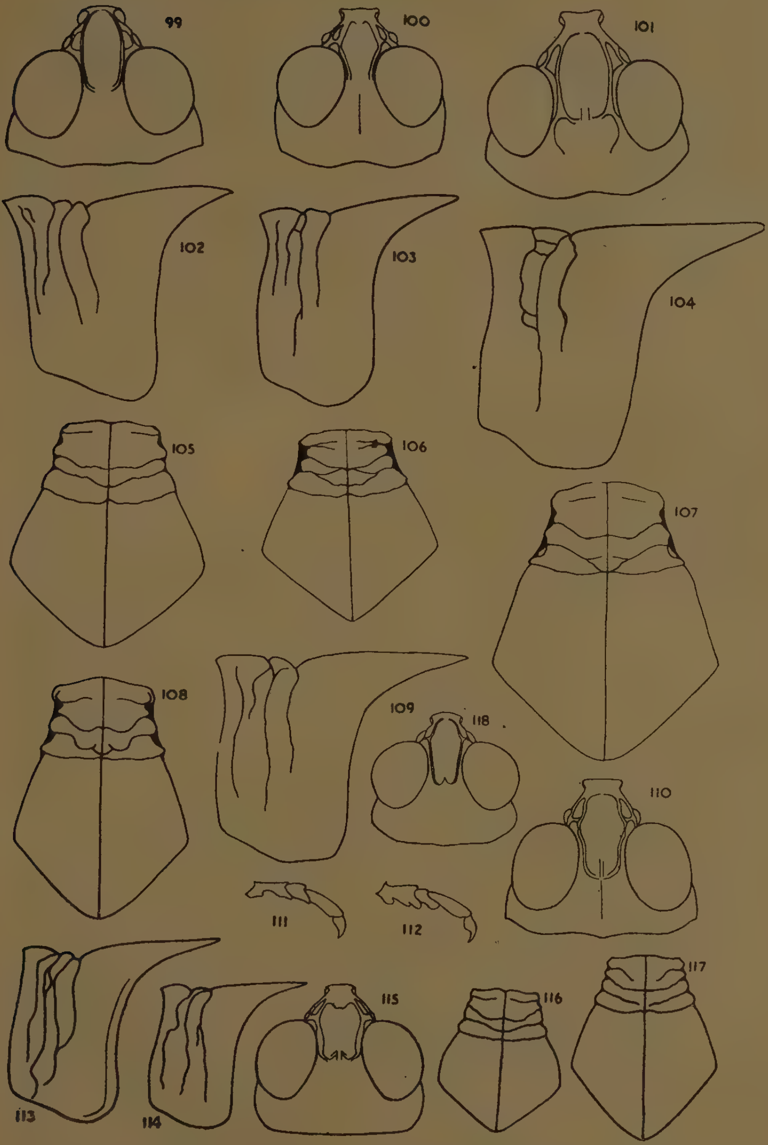
Pseudoceles obscurus (Uvarov). (Figs. 79, 80, 93.)

1927, *Thalpomena ledereri obscura* Uvarov, *Ann. Mag. nat. Hist.* (9) **20** : 198.

♂ (Paratype). Frontal ridge not concave, and weakly constricted below the ocellus, scarcely narrowed at the apex. Fastigium of vertex strongly concave with sharp, strongly curved carinae. Pronotum relatively long, slender; prozona above and on the lateral margins between sulci strongly gibbose and rugulose; metazona 1·6 times as long as



FIGS. 83–98.—Pronotum in profile : (83) *Pseudoceles ledereri* (Sauss.) ; (84) *P. armeniacus* sp. n. ; (85) *P. violaceus* (Moritz) ; (86) *P. persa* (Sauss.) ; (87) *P. zangezuri* sp. n. ; (88) *P. popovi* sp. n. ; (89) *P. ebneri* sp. n. ; (90) *P. uvarovi* sp. n. ; (91) *P. demavendi* sp. n. ; (92) *P. palaestinus* sp. n. ; (93) *P. obscurus* (Uv.) ; (94) *P. turcicus* sp. n. ; (95) *P. oedipodioides* I. Bol. ; (96) *P. arpatchai* sp. n. ; (97) *P. tari* sp. n. ; (98) *P. elbursi* sp. n.



FIGS. 99–118.—(99–101) Head above: (99) *Cophotylus steindachneri* Krauss; (100) *C. aurora* (Karny); (101) *C. iranicus* sp. n. (102–104) Pronotum in profile: (102) *Cophotylus steindachneri* Krauss; (103) *C. aurora* (Karny); (104) *C. iranicus* sp. n. (105–108) Pronotum above: (105) *Cophotylus steindachneri* Krauss; (106) *C. aurora* (Karny); (107) *C. iranicus* sp. n.; (108) *C. splendens* (Uv.). (109) *Cophotylus splendens.* Pronotum in profile. (110) Ditto. Head above. (111) *C. steindachneri* Krauss. Anterior tarsus. (112) *C. aurora* (Karny). Ditto. (113) *Crinita hirtipes* (Uv.). Pronotum in profile. (114) *C. nigripes* (Uv.). Ditto. (115) *C. hirtipes* (Uv.). Head above. (116) *C. nigripes* (Uv.). Pronotum above. (117) *C. hirtipes* (Uv.). Ditto. (118) *C. nigripes* (Uv.). Head above.

prozona, slightly raised, smooth, its lateral margins straight, moderately divergent; posterior angle obtuse, with acute apex; lower margin of lateral lobe strongly sinuate. Anterior margin of elytron at the apex obliquely truncate; membrane hard, not transparent; ratio of length to width 4·6. Hind femur relatively short, ratio of length to width 3·3. Hind knee with slightly elongate upper lobe and not deep excision.

Coloration dark, almost black; elytron without spots. Basal disc of wing intense red, not hyaline, with dark fascia and ray; apex obscure. Hind femur inside dark grey, with two light fascia, nearest to the knee more sharp; above with two indistinct dark fascia. Hind tibia above bluish.

Length of body 20; pronotum 4·5; elytron 18·3; hind femur 10·7.

♀. Like the male but larger. Lower valva of ovipositor with right angular projection on the external side.

Length of body 25; pronotum 5; elytron 20·5; hind femur 12.

Caucasus: Daghestan, Chodo-Kolo to Gidalt, 20.vii.1924, 1 ♂ (paratype), 1 ♀. Rutul, 30.viii.1924, 2 ♀ (*M. A. Riabov*).

Cophotylus Krauss. (Figs. 3, 5, 10, 14.)

1902, *Cophotylus* Krauss, *S.B. Akad. Wiss Wien*, (6) 3 : 3.

Type. *Cophotylus steindachneri* Krauss, 1902.

Of medium size, slender.

Head in profile projects above pronotum. Frons strongly oblique, straight. Frontal ridge feebly impressed at the ocellus, with inconsiderable constriction, weakly narrowed at the apex. Foveolae of vertex indistinct. Fastigium long with not very sharp carinae. Prozona of pronotum subcylindrical, constricted; its lateral margin gibbose between sulci; metazona slightly convex, its lateral margins smooth, straight, strongly divergent. Median carina interrupted by two or three sulci. Posterior angle of metazona right or obtuse. Elytron long, narrow. Vena intercalata straight or feebly sinuate. Wing long, narrow, with straight external margin. Hind femur narrow, slender. Subgenital plate short, subconical. Ovipositor short, with curved valvae; lower valva with projection on the external side.

Key to species of *Cophotylus*.

1 (4). Carinae of fastigium of vertex regularly oval (figs. 99, 101).
2 (3). Smaller. Lower margin of lateral lobe of pronotum straight (fig. 102). Basal disc of wing red . . . . *steindachneri* Krauss.
3 (2). Larger. Lower margin of lateral lobe of pronotum strongly sinuate (fig. 104). Basal disc of wing blue . . . . . **iranicus** sp. n.
4 (1). Carinae of fastigium irregularly curved (figs. 100, 110).
5 (6). Smaller. Carinae of fastigium angulate (fig. 100). Lateral margins of metazona strongly divergent; apex of posterior angle acute (fig. 106). Basal disc of wing red . . . . . . *aurora* (Karny).
6 (5). Larger. Carinae of fastigium irregularly sinuate (fig. 110). Lateral margins of metazona slightly divergent; apex of posterior angle obtuse (fig. 108). Basal disc of wing violet *splendens* (Uvarov).

Cophotylus steindachneri Krauss. (Figs. 99, 102, 105, 111.)

1902, *Cophotylus steindachneri* Krauss, *S.B. Akad. Wiss. Wien* (6) 3 : 3.

This species was described on the basis of one male; below will be found a description of the female.

♀. Very slender, of medium size.

Frontal ridge concave at the ocellus, and weakly constricted, narrowed towards apex. Fastigium strongly concave, regularly oval, with relatively sharp carinae. Lateral margin of prozona of pronotum between sulci gibbose; metazona smooth, twice as long as prozona, its lateral margins straight, strongly divergent; posterior angle obtuse, with obtuse apex; median carina interrupted by three sulci; lower margin of lateral lobe straight, oblique. Anterior and posterior margins of elytron straight; ratio of length to width 5·7. Vena intercalata slightly sinuate. Hind femur long, narrow, ratio of length to width 3·4. Hind knee with elongate upper lobe, slight excision and short lower lobe. The basal joint of anterior tarsus with broad and deep excision; basal lobe rectangular; lower lobe of the middle joint short, in profile acute at the apex. Lower valva of ovipositor with a not very large projection on the external margin. Body with sparse long pilosity.

Coloration yellowish brown; elytra with small brown spots. Basal disc of wing light scarlet, hyaline, the rest of wing colourless. Hind femur inside pale with two indistinct dark fasciae. Hind knee dark. Hind tibia above dirty yellow.

Length of body 25; pronotum 4·5; elytron 23; hind femur 11.

ARABIA: Aden, 300 ft., 24.xi.1939, 1 ♀ (*T. M. Henry*).

Cophotylus aurora (Karny). (Figs. 100, 103, 106, 112.)

1907, *Wernerella aurora* Karny, *S.B. Akad. Wiss. Wien* **116** : 355.

♂. Slender. Frontal ridge slightly concave and scarcely constricted at the ocellus, narrowed towards apex. Fastigium of vertex concave, with irregularly curved carinae and short basal carinula. Pronotum relatively short and broad; median carina interrupted by three sulci (one of them very often indistinct); lateral margin of prozona between sulci strongly gibbose; metazona twice as long as prozona, slightly raised in profile, its lateral margins straight and strongly divergent; posterior angle right, with acute apex; lower margin of lateral lobe sinuate. Elytron long; ratio of length to width 5·5; vena intercalata feebly sinuate. Hind femur slender, ratio of length to width 3·3. Upper lobe of the hind knee short, lower lobe narrow, excision shallow. The basal joint of anterior tarsus with short and narrow excision, tri-lobate, all lobes rounded; lower lobe of the middle joint in profile elongate, rounded at the apex. Body with sparse long pilosity.

Coloration yellowish brown; elytron with small brown spots. Basal disc of wing light scarlet, hyaline, the rest colourless. Hind femur inside pale with two dark fasciae; above and outside with two indistinct dark fasciae; hind knee dark. Hind tibia above yellowish, with dark ring in front of the apex and at the base.

Length of body 21; pronotum 4; elytron 20; hind femur 10.

♀. Like the male, but larger. Lower valva of ovipositor with small projection on the external side.

Length of body 24; pronotum 4·2; elytron 22; hind femur 12.

ANGLO-EGYPTIAN SUDAN: Um Darag, 2–11.vi.1933, 15 ♂, 12 ♀ (*R. C. M. Darling*).

FRENCH SUDAN: Middle Niger, Lake Horo, viii.1932, 1 ♀ (*O. B. Lean*).

Cophotylus splendens (Uvarov). (Figs. 108, 109, 110.)

1933, *Thalpomena splendens* Uvarov, *Trav. Inst. Zool. Acad. Sci. U.R.S.S.* 1 : 198.

♂ (Type). Frontal ridge concave and feebly constricted at the ocellus, weakly narrowed towards apex. Fastigium of vertex long, with irregularly curved carinae and a basal carinula. Pronotum relatively narrow; median carina interrupted by two sulci; lateral margin of prozona between sulci gibbose; metazona flat, twice as long as prozona, its lateral margins straight, slightly divergent; posterior angle right, with rounded apex; lower margin of lateral lobe convex. Elytron long, ratio of length to width 5·4. Vena intercalata straight, at the apex approximate to the radialis posterior; membrane semi-transparent. Hind femur slender, ratio of length to width 3·5. Hind knee with short upper lobe and very short lower one. Subgenital plate short, subconical obtuse at the apex.

Coloration pale yellowish; elytron without spots. Basal disc of wing light violet, hyaline, the rest colourless. Hind femur inside black, with light fascia in front of the knee; above with two indistinct dark fasciae; knee dark. Hind tibia above bluish, with indistinct dark ring in basal part.

Length of body 21; pronotum 5; elytron 21·5; hind femur 21·5.

♀ (Paratype). As the male but larger. Lower valva of ovipositor with small projection on the external margin.

Length of body 27; pronotum 6; elytron 25; hind femur 13.

BALUCHISTAN: Urak Valley, 16 miles from Quetta, 7000 ft., 8.vi.1930, 1 ♂ (type). 24.viii.1930, 1 ♂, 1 ♀. Ziavav, Juniper forest, 7500 ft., 3.v.1930, 1 ♂ (*W. H. Evans*). Quetta, 23.vii–10.viii.1929, 1 ♂ (*J. W. Evans*).

Cophotylus iranicus sp. n. (Figs. 101, 104, 107.)

♀ (Type). Slender, relatively large. Frontal ridge scarcely concave and scarcely constricted below the ocellus, narrowed towards apex. Fastigium long, oval, with not sharp carinae and with short basal carinula. Pronotum relatively long; median carina interrupted by two sulci; lateral margin of metazona between sulci gibbose; metazona flat, 2·1 times as long as prozona, its lateral margins straight, moderately divergent; posterior angle obtuse, with rounded apex; lower margin of lateral lobe strongly sinuate. Elytron long, ratio of length to width 5·2. Vena intercalata straight, at the apex approximate to the radialis posterior. Hind femur slender, ratio of length to width 3·7. Hind knee with rounded upper lobe; lower lobe shortened. Lower valva of ovipositor with moderate projection on the external side.

Coloration greyish; elytron with dark small spots. Basal disc of wing light blue, hyaline. Hind femur inside black, with two light fasciae, the nearer to the base incomplete; above and outside with two indistinct dark fasciae. Hind tibia above bluish.

Length of body 25; pronotum 5·5; elytron 26; hind femur 14.

SOUTH PERSIA: Deh-Bala, 29.vii.1935, 3 ♀ (including type) (*H. E. Biggs*).

Crinita gen. n. (Figs. 4, 11.)

Type. *Thalpomena hirtipes* Uvarov, 1923.

Of small or medium size, slender. Head in profile projects strongly above the pronotum, rather inflated. Frons oblique, convex. Frontal ridge with raised margins; weakly concave below the ocellus, narrowed towards apex; in profile slightly impressed in front of the fastigium. Foveolae of vertex flat. Fastigium elongate, feebly concave its carinae not sharp. Eyes strongly convex. Pronotum slightly constricted in prozona; median carina thin, linear, interrupted by three sulci; lateral margin of prozona between sulci gibbose; metazona smooth, its lateral margins divergent. Elytron long; vena intercalata distinct, sinuate, at the apex approximate to and almost touching vena radialis posterior; reticulation very sparse, membrane thin, hyaline. Wing hyaline, its membrane very thin, shiny. Subgenital plate of male short, subconical, obtuse at the apex. Ovipositor short, slender, its valvae feebly curved; lower valva with projection on the external margin.

This genus differs sharply from the nearest genera, *Cophotylus* and *Sphingonotus* by the very sparse reticulation of the elytra.

Crinita hirtipes (Uvarov). (Figs. 113, 115, 117.)

1923, *Thalpomena hirtipes* Uvarov, *Ent. mon. Mag.* 59 : 84.

♂. Of medium size. Frontal ridge feebly concave and weakly constricted below the ocellus, narrowed towards apex. Fastigium feebly concave, at the apex slightly broader than at the base, with irregularly curved carinae. Pronotum moderately long, in profile slightly impressed between sulci; lateral margin of prozona moderately gibbose between sulci; metazona smooth, flat, 2·3 times as long as prozona, its lateral margins almost straight; posterior angle acute, with acute apex. Lower margin of lateral lobe almost straight (scarcely sinuate). Elytron long, its anterior and posterior margins straight, ratio of length to width 5·4. Hind femur slender; ratio of length to width 3·7. Hind knee short, broad, with elongate upper lobe and deep excision. Body, particularly below, with dense long pilosity.

Coloration pale yellowish grey; elytron with small dark spots. Wing hyaline, shiny. Hind femur inside pale, with two dark fasciae; above and outside with two indistinct dark fasciae. Hind knee dark. Hind tibia greyish blue, with dark ring at the apex.

Length of body 19; pronotum 4; elytron 19; hind femur 9.

♀ (Type). Like the male but slightly larger. Lower valva of ovipositor with small rounded projection on the external margin.

Length of body 20; pronotum 4; elytron 20; hind femur 11.

PALESTINE: Jericho, 14.x.1922, 1 ♀ (type) (*P. A. Buxton*). 25.vii.1935, 1 ♂. Jerusalem, 7.xi.1935, 3 ♂, 1 ♀. vii–viii.1929, 7 ♂, 5 ♀ (*S. Shershersky*). Wadi Kelt, nr. Jerusalem, 28.vi.1925, 1 ♂ (*F. S. Bodenheimer*).

TRANSJORDANIA: Petra, 24–27.vi.1945, 1 ♂, 2 ♀ (*R. A. Crosby*).

Crinita nigripes (Uvarov). (Figs. 114, 116, 118.)

1929, *Thalpomena hirtipes nigripes* Uvarov, *Ergebn. Sinai Exped. Leipzig.* : 94, figs. 1–2.

♂ (Type). Small and slender. Frons strongly oblique (angle 45°). Frontal ridge scarcely concave and scarcely constricted at the ocellus, at the apex strongly narrowed. Fastigium of vertex feebly concave, with fine, oval, weakly curved carinae. Pronotum relatively short; lateral margin of prozona between sulci slightly gibbose; metazona flat, smooth, 1·8 times as long as prozona, its lateral margins smooth, concave and relatively strongly divergent; posterior angle obtuse, its apex obtuse. Elytron long, ratio of length to width 5·4; membrane thin, hyaline. Membrane of wing thin, shiny. Hind femur slender, ratio of length to width 3·3. Hind knee short, broad, its upper lobe slightly elongate, excision deep and narrow. Body with long sparse pilosity.

Coloration yellowish grey; elytron with small dark spots. Wing hyaline, faintly bluish at the base, with dark venation, at the apex slightly infumate. Hind femur inside dark, with two light fasciae; above and outside with two indistinct dark fasciae. Hind knee dark. Hind tibia above dark blackish.

Length of body 17; pronotum 3; elytron 16; hind femur 7.

SINAI: Katherine Kloster, 1 ♂ (type) (*F. S. Bodenheimer*).

Vol. 100. Part 14. Pp. 393–409, 3 figs. 30th December, 1949

En. 344

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CONTENTS

PAGE

BRIAN, M. V., and BRIAN, A. D. Observations on the taxonomy of the Ants *Myrmica rubra* L. and *M. laevinodis* Nylander. (Hymenoptera: FORMICIDAE.) . . . 393–409, 3 figs.

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OBSERVATIONS ON THE TAXONOMY OF THE ANTS *MYRMICA RUBRA* L. AND *M. LAEVINODIS* NYLANDER. (HYMENOPTERA: FORMICIDAE.)

By M. V. Brian and A. D. Brian.
(*Department of Zoology, Glasgow University.*)

Manuscript received 14th April, 1949.
(Read 1st June, 1949.)

With 3 Text-figures.

1. Distinction Between *Myrmica rubra* L. and *M. laevinodis* Nylander.

The species *Myrmica rubra* L. was divided by Nylander (1846) into three forms; of the two with curved scapes, one having workers with longer epinotal spines and a wrinkled area between was called *M. ruginodis*, and the other having smaller epinotal spines and a smooth area between was called *M. laevinodis* Nylander[1]. Numerous ants which would not fit into either type were classed as intermediates by Forel (1874) under the title *M. laevinodis* Nylander var. *ruginodo-laevinodis* Forel.

Nylander's distinction is satisfactory only if spine-length is assessed relative to head-width and a sample of the workers of a colony examined. These precautions are necessary for two reasons: first, because within each species colony mean spine-length increases with colony mean head-width, and *laevinodis* colonies of large workers[2] may have spines as long as *rubra* colonies of small workers. This means that by taking head-width into account in assessing spine-length, colonies which would have been classed as intermediate solely on a basis of spine-length fall definitely into one or other species group, being *laevinodis* if they have large heads, and *rubra* if they have small heads. The second precaution is necessary since individual workers from colonies of distinct species may be indistinguishable.

A sample of 25 workers was taken from each colony examined. Head-width was measured immediately behind the eyes, and spine-length as in fig. 1. When the average values of these for each nest were plotted graphically (fig. 2), they formed two distinct groups each showing internal regression of one character on the other. Details are set out in Table I.

Care has been taken to include in this survey specimens which Mr. Donisthorpe[3] considered typical and specimens which he said would fall into Forel's intermediate category. After measurement the former proved to be, in relation to our collection, extreme in type, the *rubra* having large spines for its head-width (which was large), and the *laevinodis* small spines for its head-width (which was small). The intermediates fell in the *laevinodis* group. We also sent Mr. Donisthorpe samples of the nests marked with circles in fig. 2. These he said would fall into Forel's category but were "nearer *rubra.*" Reasonable care has thus been taken to make the study as comprehensive as possible.

---

[1] Santschi (1931) has maintained that Linnaeus was describing *M. ruginodis* Nyl. when he formed the species *M. rubra* L., and that the latter name has precedence. Santschi's nomenclature is used in this paper.

[2] Mean head-width (y) regresses on mean weight (x): for *rubra*, $y = \cdot 0840x + \cdot 8301$ where the standard error of the regression coefficient $= \cdot 0245$ millimetres per milligram.

[3] We wish to acknowledge the help which Mr. Donisthorpe kindly gave by both lending specimens from his collection and examining a number of our own.

Compared with the measurement method of discrimination, the use of the rugosity character was inferior, partly because of the difficulty of making a clear distinction between wrinkled and smooth, and also because of the lack of consistence between the two methods. The workers from each of 22 nests assigned to the group *rubra* by measurement criteria were examined; of these 7 nests contained some workers with the area between the epinotal spines smooth (Table III), but these individuals did not have especially short spines. One nest which fell well within the *rubra* group (head-width 34 divisions = 1·030 mm., spine-length 27·6 divisions = ·380 mm.) had a majority of smooth workers in the sample. The position in *laevinodis* was less variable: of 180 workers from 18 nests, only 4 from 3 nests showed any sign of wrinkles. These were all of moderate spine-length, but many with larger spines were quite smooth. Thus in neither species did the character show any relation to spine-length. Nevertheless, discrimination by this method would in most cases

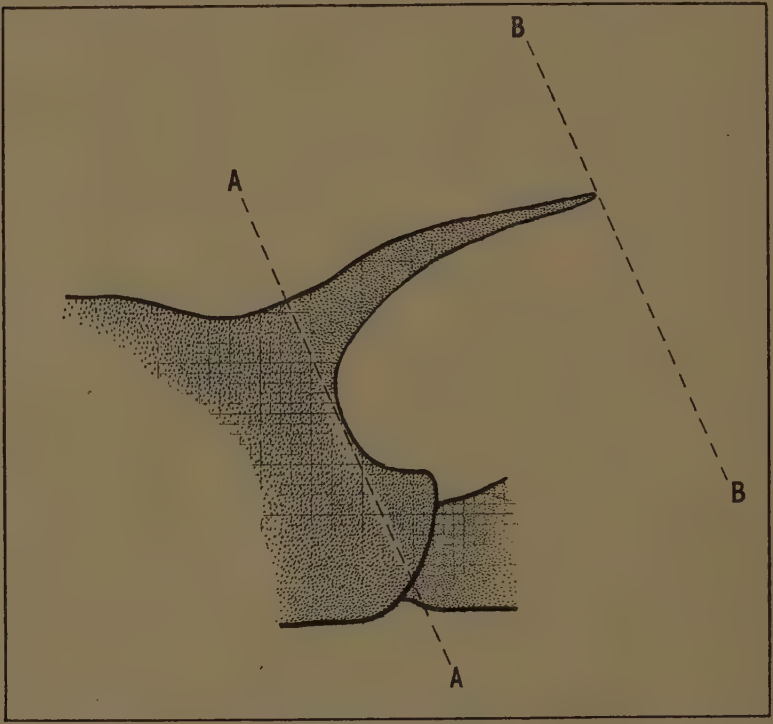

Fig. 1.—Spine of *M. rubra* ☿ from left side measured from A to B.

agree with the measurement method in distinguishing colonies with all or a majority of workers rugose (*rubra*) from colonies with all or a majority of their workers smooth (*laevinodis*), and it has one point in its favour—it can be used in the field with a hand lens.

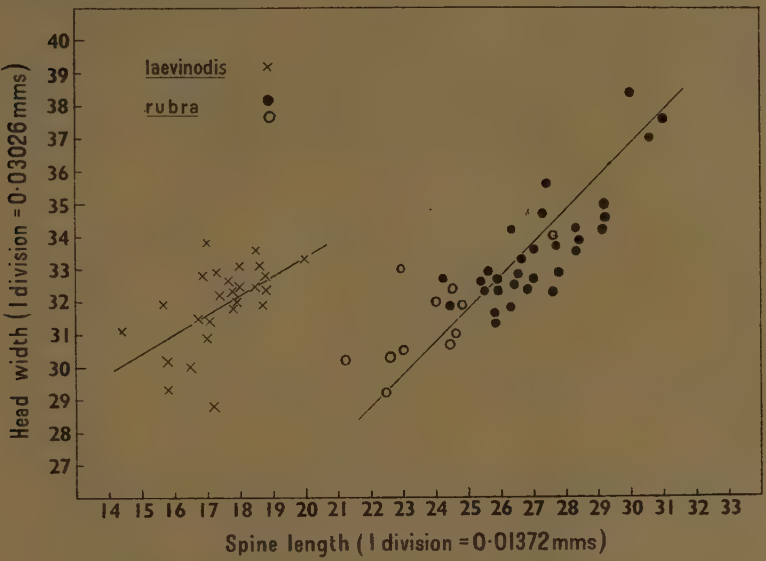

Fig. 2.—Relation of average worker head-width and spine-length in colonies of *M. laevinodis* and *M. rubra* showing regression lines.

Table I.—*Average Head-width and Average Spine-length in Millimetres, for Samples of* 25 *Workers from each of* 26 laevinodis *and* 42 rubra *Colonies Taken in Various Parts of the British Isles.*

	laevinodis.	*rubra.*
Mean head-width (x)	0·9665	0·9989
„ spine-length (y)	0·2397	0·3611
Correlation coefficients	0·8093 ($< 1\% P$)	0·8528 ($< 1\% P$)
Regression equations	$y = \cdot 2489x - \cdot 0009$	$y = \cdot 4593x - \cdot 0977$
S.E. of regression coefficients	0·03687	0·04449

Localities :

laevinodis :	3	colonies from	Glen Falloch, Perthshire.
	6	„ „	Ings, Westmorland.
	4	„ „	Great Barrow, Cheshire.
	3	„ „	Earlswood, Warwickshire.
	10	„ „	Harpenden, Hertfordshire.
rubra :	3	colonies from	Glen Falloch, Perthshire.
	26	„ „	Colgrain, Dumbartonshire.
	8	„ „	Ings, Westmorland.
	3	„ „	Delamere Forest, Cheshire.
	2	„ „	Harpenden, Hertfordshire.

TABLE II.—*The Frequencies of each Head-width, Spine-length Combination in* 1025 *Workers of* rubra (*from* 41 *colonies*) *and* 650 *Workers of* laevinodis (*from* 26 *Colonies*), *considered without regard to Colony Relationship. The data are grouped according to micrometer divisions: for head-width,* 1 *division* = ·03026 *mm.; for spine-length,* 1 *division* = ·01372 *mm.;* laevinodis *in italics.*

Spine-lengths.	Head-width.															
	26.	27.	28.	29.	30.	31.	32.	33.	34.	35.	36.	37.	38.	39.	40.	41.
11	.	.	*1*	.	.	.	.	.	.	.	.	.	.	.	.	.
12	*1*	.	.	*2*	*2*	.	.	.	.	.	.	.	.	.	.	.
13	.	.	.	*5*	*4*	*1*	*6*	.	.	.	.	.	.	.	.	.
14	*1*	*3*	*1*	*6*	*1*	*9*	*3*	*3*	*1*	.	.	.	.	.	.	.
15	.	.	*5*	*10*	*8*	*10*	*13*	*7*	*2*	.	.	.	.	.	.	.
16	.	*3*	*2*	*6*	*9*	*26*	*19*	*16*	*9*	*1*	*2*	.	.	.	.	.
17	.	.	*7*	*5*	*16*	*19*	*49*	*22*	*17*	*3*	*2*	.	.	.	.	.
	1	.	1													
18	.	.	*1*	*6*	*12*	*16*	*25*	*25*	*10*	*3*	*2*	*1*	.	.	.	.
	1				1											
19	.	.	*3*	*3*	*6*	*11*	*15*	*18*	*19*	*4*	*1*	*1*	.	.	.	.
						1										
20	.	.	*1*	.	*4*	*14*	*20*	*15*	*13*	*8*	*1*	*1*	.	.	.	.
				2	1	1	1	1								
21	.	.	.	.	*2*	*1*	*7*	*7*	*9*	*4*	*2*	.	.	.	.	.
			2	6	8	10	7	7								
22	.	.	.	.	.	*1*	*3*	*1*	*4*	*2*	.	.	.	.	.	.
		1	3	6	8	10	7	5	1	.	1					
23	.	.	.	*1*	.	.	.	*1*	*1*	*3*	.	.	.	.	.	.
				7	11	16	15	9	2	1						
24	.	.	.	.	.	.	.	*2*	.	.	*1*	*1*	.	.	.	.
			2	1	7	12	19	9	7	1						
25	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
				3	8	22	28	25	10	6	1					
26	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
					4	17	29	49	26	15	1	1				
27	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
					3	10	42	33	45	17	9	1	2	1		
28	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
					1	3	10	25	38	17	8	5	.	1		
29	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
					1	1	10	11	28	22	12	9	4	2		
30	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
						2	4	10	15	31	12	7	4	2	1	
31	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
								5	6	10	17	5	11	1	.	1
32	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
									3	5	6	8	6	.	1	
33	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
										1	4	3	2	3		
34	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
										1	2	.	2	1		
35	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
											1	1	.	.	1	
36	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
37	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
													1	.	.	1

It will be noticed that mean head-size did not differ very much, but that mean spine-length did ; also that the slope of the *rubra* line was greater than that of *laevinodis*, but the significance of this is not clear.

Although the regression groups remain reasonably discrete when based on colony means, they intermingle slightly when individual workers are considered. The extent of this may be seen from Table II.

TABLE III.—*Showing the Frequency with which a Sample of* 10 *Workers from each of* 22 rubra *and* 18 laevinodis *Colonies Contained* 0 *to* 10 *Specimens having the Area between the Epinotal Spines Smooth.*

Number with smooth area.	*rubra.*	*laevinodis.*
10	—	15
9	—	2
8	—	1
7	1*	—
6	—	—
5	—	—
4	—	—
3	1	—
2	2	—
1	3	—
0	15	—
	22	18

* By dimensions this was clearly a *rubra* colony (head-width, 34 divisions = 1·030 mm., spine-length 27·6 divisions = ·380 mm.).

Other differences between the two species are more conveniently mentioned in the third section of this paper.

2. VARIATION WITHIN *M. rubra* L.

Suspicions that the species *rubra* was heterogeneous were aroused in the early stages of experimental sociological studies. These were later confirmed, and it was found that there existed two forms, each self-propagating, which may be briefly contrasted and named as follows :

> var. **macrogyna** var. nov.: females and males larger, colonies usually monogynous with relatively large aggressive workers, the average worker head-width less than the average female head-width, colony reproduction by dissemination of fertile females which found colonies either alone or in small aggregates ;
>
> var. **microgyna** var. nov.: females and males smaller, colonies polygynous with relatively small and docile workers, the average worker head-width similar to the average female head-width, fertile females return to their nest (and possibly other nests) and colonies reproduce by fission.

The two forms are not sharply distinct, but intermediates are rare in comparison with the types. The evidence for these statements will now be presented.

(a) *Head-width Measurements of Queens.*

Colonies were collected, the queens (deälate females) removed and counted and the width of their heads measured. The results are set out in Table IV and illustrated in fig. 3.

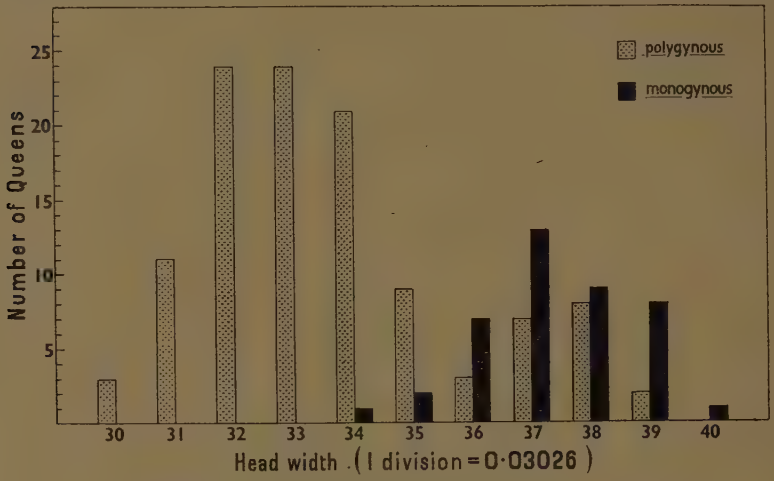

Fig. 3.—Head-width distribution of queens from polygynous and monogynous colonies of *M. rubra.*

Table IV.—*Head-width Frequencies of Queens in* 23 *Polygynous* (2–15 *Queens per Nest*) *and* 41 *Monogynous Colonies of* M. rubra. *Head-widths in micrometer divisions* (1 *division* = ·03026 *mm.*)

	Head-width.											Total.
	30.	31.	32.	33.	34	35.	36.	37.	38.	39.	40.	
Polygynous	3	11	24	24	21	9	3	7	8	2	.	112
Monogynous	.	.	.	.	1	2	7	13	9	8	1	41
Total	3	11	24	24	22	11	10	20	17	10	1	153

A tendency towards an association of monogyny with macrogyny, and polygyny with microgyny[4] is apparent. The combined results from the 64 nests show a bimodal frequency distribution, the medium head-widths being rarer than either larger or smaller ones.

The slight rise in frequency of the larger head sizes in polygynous nests is at first difficult to interpret. We believe it to be caused by the fact that *macrogyna* queens sometimes associate in colony-founding (primary pleometrose, Wasmann, 1910) and do not separate when workers are produced (as happens, for example, in *Lasius niger* Linn.), but it is possible that an alternative explanation, that queens may sometimes gain access to nests which already possess one (secondary pleometrose), may supplement the first. Our contention is supported by two lines of evidence: first, that groups of freshly fecundated *macrogyna* queens set together in observation nests lived and reared workers amicably, and secondly, that quite a close parallel exists between the frequencies with which groups of 1, 2, 3, 4, etc., queens are found in process of colony-founding and the frequencies with which these numbers of queens are associated in mature colonies (Table V).

---

[4] The small queens, as will be shown later, have workers whose average head-width is slightly larger than their own, so that they are properly called microgynes in the conventional sense of that word, being females as small as or smaller than their workers.

TABLE V.—*An Analysis of 35 Colony-founding Groups of Queens to Show Head-width (1 division = ·03026 mm.) and Group-size Frequencies. For Comparison, Queen Group-size Frequencies in 43 Mature* macrogyna* *Colonies are given.*

Size of Group.	Head-widths.								Number of groups.	Number of mature nests with 1, 2, 3, etc., queens.
	33.	34.	35.	36.	37.	38.	39.	40.		
1	.	1	1	7	9	5	6	1	30	38
2	.	.	.	1	2	1	2	.	3	1
3	.	.	.	.	.	.	.	.	0	2
4	.	.	.	.	2	1	.	1	1	1
5	.	.	.	.	.	.	.	.	0	0
6	1	2	1	1	1	.	.	.	1	1
	1	3	2	9	14	7	8	2	35	43

* That is, where all queens present, if more than one, exceeded 36 divisions in head-width.

Since very few *microgyna* females were discovered in autumn in process of founding colonies, it was reasonable to suppose that their normal habit was to return to mature nests of their own type. This was confirmed by examination of queens in *microgyna* nests in autumn. Dissection showed that they fell into two categories, one having ovaries with well developed yolky oocytes and terminal *corpora lutea*—the old laying queens—and the other having moderately yolky oocytes but no *corpora lutea*—the young queens added since the nuptials, whose ovaries had developed a little, but not ovulated.[5]

Further confirmation of these results was obtained experimentally.

(b) *Experimental Introduction of Queens.*

Recently fecundated females of a range of head-sizes were added to queenless colonies of both *macrogyna* and *microgyna* types in observation nests and the reactions noted. Six colonies, three of each type were used, each consisting of about 50 workers and brood. Six queens, of each head-width from 34 to 39 divisions, were added three at a time to each nest. Reactions were usually definite, and it was not necessary to leave the queens in for more than a few minutes. Either they were attacked immediately by workers with opened mandibles, and dragged about relentlessly, or they were quickly examined, given food, and allowed to brood. But in certain cases, a worker, on approaching an introduced queen, opened its mandibles without attacking, and after a pause, went away. This we have described as "menacing," but we think it probably results from an interaction between the intensity of stimulation and the constitutional peculiarities of the subject, being evoked by normal stimulation of a constitutionally unaggressive worker, or under-stimulation of a constitutionally normal worker. These results are set out in Table VI.

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[5] It is usual in *M. rubra macrogyna* for young queens to begin laying in the spring following nuptials (in contrast to *Lasius niger* and *L. flavus*), but on one occasion we have found a group of queens with a single egg.

TABLE VI.—*Queen Introduction Experiments: 6 Early Post-nuptial Females of each Head-size were Added in Two Separate Groups of* 3, *to each of* 3 macrogyna *and* 3 microgyna *Groups of Workers and Brood. In each column of the Table, Numbers Tolerated, Menaced, and Attacked, are set out so : T, M, A.*

Head-width of female.	Three *macrogyna* groups.			Three *microgyna* groups.		
	1.	2.	3.	1.	2.	3.
39 and over . . .	4–1–1	3–0–3	3–1–2	0–0–6	0–1–5	0–0–6
38	1–2–3	0–2–4	1–2–3	0–0–6	0–0–6	0–2–4
37	3–3–0	0–2–4	4–2–0	0–0–6	0–0–6	0–3–3
36	3–0–3	0–0–6	1–1–4	2–2–2	3–0–3	2–2–2
35	0–0–6	0–0–6	0–0–6	6–0–0	6–0–0	6–0–0
34 and less . . .	0–0–6	0–0–6	0–1–5	6–0–0	6–0–0	6–0–0

These results very clearly confirm the existence of two varieties. We may note the following points:

(1) Groups of workers within each type differed slightly in their reactions.

Thus *macrogyna* 2 were relatively aggressive, whilst *microgyna* 3 were relatively tolerant.

(2) All *macrogyna* rejected queens of 35 and less divisions whereas all *microgyna* accepted them.

(3) *Microgyna* attacked all queens of greater head-width than 36 divisions, but *macrogyna*, instead of accepting them as might at first be expected, rejected sometimes and accepted at other times. Perhaps this is due to an unnatural circumstance, for we have good reason to suppose that large queens do not usually attempt to re-enter mature colonies.

(4) Intermediate behaviour was shown towards queens of head-width 36 divisions by all groups except group 2 *macrogyna* which was an aggressive type. This may indicate that the change in ant-perceptible character[6] takes place gradually within the head-size 36, and that a queen of this size only evokes aggressive behaviour in hostilely disposed workers.

(5) On the other hand, the narrowness of the transition belt is surprising, and the possibility that two types are included in the size 36 cannot be dismissed. This was the subject of a further experiment reported in a later section.

(c) *Experimental Mixing of Workers.*

Workers of like and unlike varieties were mixed on a number of occasions using each time 10 of each. After 2 minutes the number fighting was recorded. These results are summarized in Table VII.

[6] Observations indicate that perception is made without contact, at a distance of a few millimetres, thus indicating an olfactory mechanism.

TABLE VII.—*Workers of the Two Varieties* microgyna *and* macrogyna *were Mixed:* 10 *of Each Type* (*but from different Colonies*) *were used, and the Number Fighting after* 2 *Minutes Recorded. Below are Shown the Proportion of Cases in which No Fighting Took Place.*

	Macrogyna with *macrogyna.*	*Macrogyna* with *microgyna.*	*Microgyna* with *microgyna.*
Number of tests	16	19	19
„ with no fighting . .	4	1	15

They clearly indicate that mixing of dissimilar types gives the greatest chance of antagonism.[7] But, whereas mixtures of *microgyna* workers were usually peaceful, mixtures of *macrogyna* usually resulted in combat. In this respect, striking consonance was shown with the results of introducing queens. Thus, the *macrogyna* were frequently intolerant of both queens and workers of their own type. It is possible that the underlying cause may prove to be due to the existence of genetically differing strains, each type passed from queen to worker progeny, but it is also quite likely that the preponderance of antagonistic reactions is the result of living in separate isolated colonies derived from single queens. The *microgyna*, habituated to rather diverse associates in their polygynous nests, were as a rule tolerant of queens and workers of their own variety, but strongly intolerant of those of the other kind.

(d) *Special Consideration of Intermediates.*

As some of the principal characters of the two varieties have been contrasted, it is important now to consider the intermediates.

Queens of Head-width 36 *Divisions* (= 1·090 *mm.*).

Queens of this head-size have been found behaving as *macrogyna* more often than as *microgyna*. As *macrogyna* we have the following cases: 7 specimens were the sole queens in nests, and 1 specimen was associated with two larger queens in a 3-queen *macrogyna* nest (Table IV); 7 queens have been found alone and 1 with a larger queen presumably colony-founding (Table V); 1 queen was found in a 6-queen aggregate of which 1 was larger and 4 were smaller (Table V). Of queens behaving as *microgyna* we have only 2 specimens associated with smaller queens in polygynous colonies (part of Table IV).

In queen introduction experiments (Table VI) it was noted that *microgyna* workers rejected a large proportion of these queens, and *macrogyna* workers accepted a few. Worker reaction to this head-size was specially investigated, using the same 6 nests as before (3 of each variety). Fourteen queens were introduced separately giving a total of 42 test reactions for each *rubra* type (Table VIII).

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[7] Statistical analysis might proceed as follows:

(1) Comparison of column 2 with column 3: 16 cases of no fighting would be expected divided evenly between the two groups if no bias, $\chi^2 = 12 \cdot 25$, < 1 per cent. *P.*

(2) Comparison of column 1 with column 3: 19 cases of no fighting would divide in the ratio 19/16 if no bias, $\chi^2 = 4 \cdot 66$, 1–5 per cent. *P.*

(3) Comparison of column 1 with column 2: 5 cases of no fighting would divide in the ratio 16/19 if no bias, $\chi^2 = 2 \cdot 36$, 10–20 per cent. *P.*

Table VIII.—*The Reactions of* 3 microgyna *and* 3 macrogyna *Groups of Workers and Brood to* 14 *Queens of Head-width* 36 *Divisions* (= 1·090 *mm.*) *were Tested by Adding each Queen Separately: T = tolerated, M = menaced, A = attacked.*

Queen number.	Three *microgyna* groups.			Three *macrogyna* groups.		
	1,	2,	3,	1,	2,	3,
4	T	T	T	T	A	A
8	T	M	T	A	A	A
6	M	T	M	A	A	A
1	M	A	M	T	A	M
11	M	A	M	M	M	T
9	A	M	A	M	M	M
10	A	A	M	T	T	M
12	A	A	M	M	M	A
2	A	A	A	T	T	T
3	A	A	A	T	A	T
13	A	A	A	T	M	A
14	A	A	A	A	M	A
5	A	A	A	A	M	A
7	A	A	A	T	M	M

It will be noticed that no queen which was tolerated by one group of *microgyna* was attacked by another group. Menacing appears as an intermediate form of behaviour, and it is possible to arrange the queens in a series from those unanimously tolerated to those unanimously attacked, as has been done in the table. When this is done on a basis of reactions by *microgyna*, a certain order appears in the, at first sight, chaotic reactions of the *macrogyna* groups; the first three queens, which may be described as "tending to be tolerated" by the *microgyna*, are seen to be very much more consistently attacked than the others. These results thus come into line with earlier ones in which a wider range of head-size was used, and, in fact it is evidence that within this single head-width group a gradual transition from *microgyna* to *macrogyna* occurs, and that it contains more of the latter type.

Since queens exist towards which reaction is intermediate, we may reasonably regard this as strong evidence that the *rubra* species is composed of two forms connected by transition types, rather than by two forms distinct in ant-recognizable characters, but of overlapping head-widths.

Queens of head-width 35 *divisions* (= 1·060 *mm.*).

Most of the queens in this class behaved as *microgyna*. We have the following cases: 9 specimens were associated with smaller queens in polygynous colonies (Table IV). Queens behaving as *macrogyna* were as follows: 2 specimens were the sole queens in mature colonies (Table IV), 1 specimen was found alone, and 1 in the aggregate of 6 queens already referred to (Table V), which were presumed to be founding colonies. In queen introduction experiments (Table VI), they were consistently accepted by *microgyna*, and rejected by *macrogyna*.

(e) *Exceptional Cases: Atypical Behaviour.*

A few exceptional cases should be noted. One queen of head-width 33 divisions was discovered in a colony-founding aggregate (Table V), whereas in 24 other cases of the same size queens were in polygynous colonies of *microgyna*. In this same curious aggregate there were 2 queens size 34 divisions, and another queen of this size has been discovered alone, but in 21 other cases they have been queens in colonies with smaller queens. One large queen (head-width 37 divisions) was collected with 3 definitely *microgyna* queens in a mature colony, whereas in 19 other cases this size have been either alone or with larger queens in fully developed colonies.

(f) *The Relation between Head-widths of Queens and Winged Females in the Same Nest.*

The measurements to be described indicated that each variety tended to be self-propagating, though (if head-width criteria are to be trusted) cases were found where both types arose from a single queen.

In 10 colonies of *macrogyna* examined, a close correlation existed between the head-width of the queen and the average of 25 virgins ($r = +\cdot 9126$, < 1 per cent. P). The equation of the linear regression was $y = \cdot 9302x + \cdot 081$, where y is the average virgin head-width, and x the head-width of the queen, both measured in millimetres (S.E. of regression coefficient = ·1473 mm.). The average head-width of queens, 1·117 mm., differed little from the average for all virgins, 1·120 mm. The frequency distributions of the virgin head-widths are shown in Table IX.

TABLE IX.—*Frequency Distributions of Female Head-widths in Micrometer Divisions* (1 *division* = ·03026 *mm.*), *from* 10 macrogyna *Colonies.*

Head-width.	Colony number.									
	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.
33	6	.	.	.	.	.	.	.	.	.
34	5	.	.	.	.	.	.	.	.	.
35	10*	5	1	4	.	1	.	.	.	.
36	4	16*	12*	11*	4	2	1	.	.	.
37	.	4	12	8	3*	5*	16*	5	.	5
38	.	.	.	2	3	13	8	17*	9*	12
39	.	.	.	.	.	4	.	3	10	8*
40	.	.	.	.	.	.	.	.	1	.
41	.	.	.	.	.	.	.	.	1	.

* Head-width of queen.

It will be noted that dispersion was usually small. Also that in 3 cases out of 10 the queen's size was not the modal one, and in 4 of the 7 cases where it was, the distribution was asymmetrical. We may, perhaps, look to the unknown male parent or parents for the explanation of this.

With *microgyna*, no correlation was obtained between the average head-widths of virgins and of queens from the same nest. This is not surprising, in view of the heterogeneity of queen head-size in each nest. But it is probable that a similar relation exists for small as for large queens (see, for example, the instance of colony 1 in Table IX). The frequency distributions of virgin head-width are shown in Table X, that of the queens being included as well. In colony 1 it would seem likely that only one queen has been instrumental in forming female progeny. The average head-widths of queens, 0·995 mm., was similar to that of virgins, 0·985 mm.

Table X.—*Frequency Distributions of Virgin Female (V) and Queen (Q). Head-widths in* 6 microgyna *Colonies, in Micrometer Divisions,* (1 *division* = ·03026 *mm.*)

Head-width.	Nest numbers.											
	1.		2.		3.		4.		5.		6.	
	V.	Q.	V.	Q.	V.	Q.	V.	Q.	V.	Q.	V.	Q.
30	5	.	.	.	1	.	.	.	.	.	.	.
31	9	1	2	1	4	1	1	.	.	.	.	.
32	2	.	11	1	10	1	6	2	5	4	2	.
33	.	3	4	1	8	1	8	3	14	3	5	.
34	.	2	.	.	2	.	1	.	5	1	11	1
35	.	.	.	.	.	.	.	.	1	.	7	1
36	.	1	.	.	.	.	.	.	.	.	.	.

(g) *The Relation between Head-widths of Queens and Workers in the Same Nest.*

Macrogyna showed a good correlation between queen and average worker head-widths ($r = +\cdot 6740$, < 1 per cent. P). The workers were on the average smaller than their queens, averaging 1·069 mm. (= 35·34 divisions) as opposed to 1·113 mm. (= 36·78 divisions). The regression equation was $y = \cdot 817\,x + \cdot 160$, where y is the expected average head-width of workers, and x the actual head-width of the queen, both in millimetres (S.E. of regression coefficient = ·0258 mm.). The variation of worker size in each colony was greater than that of virgins (Table XI).

Table XI.—*Frequency Distributions of Worker Head-widths in* 10 *Colonies of* macrogyna, *in Micrometer Divisions* (1 *division* = ·03026 *mm.*).

Head-width.	Nest number.									
	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.
30	1	.	.	.	.	.	.	.	.	.
31	4	.	.	.	.	.	.	.	.	.
32	14	1	2	.	1	.	.	.	.	.
33	15	5	8	3	5	.	1	.	.	1
34	9	5	8	9	12	2	.	2	.	.
35	3*	11	7	14	17	5	5	8	.	2
36	4	2*	*	15	12	14	12	8	5	4
37	.	.	.	8*	3*	14*	5*	7	8	1
38	.	1	.	1	.	12	2	*	8*	12
39	.	.	.	.	.	3	.	.	4	5*

* Head-width of queen.

For *microgyna*, no correlation could be detected between mean worker and mean queen head-width. The workers were on the whole smaller than those of *macrogyna*. They averaged 1·005 mm. (= 33·2 divisions), and were thus just a little larger than their queens, which averaged 0·995 mm. (=32·9 divisions). In this respect they contrast with *macrogyna*, and are microgynes in the conventional sense of the word.[8] The frequency distributions of head-width for workers and queens from 10 colonies are shown in Table XII .

TABLE XII.—*Head-width Frequencies in Workers (W) and Queens (Q) from 10 Colonies of* microgyna, *in Micrometer Divisions* (1 *division* = ·03026 *mm.*).

Head-width.	Number of colony.																			
	1.		2.		3.		4.		5.		6.		7.		8.		9.		10.	
	W.	Q.	W.	Q.	W.	Q.	W.	Q.	W.	Q.	W.	Q.	W.	Q.	W.	Q.	W.	Q.	W.	Q.
28	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.
29	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4	.
30	.	.	.	.	.	.	2	.	1	.	1	1	.	.	.	.	.	.	4	.
31	1	.	.	.	4	.	1	1	6	.	3	2	1	.	2	.	2	.	5	4
32	8	4	1	.	4	.	4	1	3	2	6	5	1	1	8	4	6	1	6	2
33	5	3	.	.	12	3	11	1	7	[illegible]	12	4	1	3	9	.	8	.	4	1
34	8	1	3	1	4	2	6	.	3	.	3	2	11	1	4	.	6	.	.	.
35	1	.	7	1	.	.	.	.	2	.	.	.	7	.	1	.	3	1	.	.
36	.	.	10	.	1	1	1	.	3	.	.	.	3	.	1	.	.	1	1	.
37	1	.	3	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.
38	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

(h) *The Head-widths of Males.*

Microgyna males averaged less than *macrogyna* males, ·910 mm. (= 30·12 divisions) instead of ·980 mm. (= 32·42 divisions), but the difference was so small compared with the variability that the frequency distributions overlapped (Table XIII), and when combined gave little sign of bimodality, as did the female distributions. The total male range of size was less than the female range, 8 divisions (·2421 mm.) instead of 10 divisions (·3026 mm.).

TABLE XIII.—*Head-width Frequency Distributions of Males from* 5 macrogyna *and* 5 microgyna *Colonies in Micrometer Divisions* (1 *division* = ·03026 *mm.*).

Head-width.	Five *microgyna* colonies.					Five *macrogyna* colonies.					Total.
	1.	2.	3.	4.	5.	1.	2.	3.	4.	5.	
27	1	.	.	.	.	.	.	.	.	.	1
28	5	2	.	.	.	1	.	.	.	.	8
29	12	9	2	1	1	2	.	.	.	.	27
30	6	10	3	6	9	6	3	.	.	.	43
31	1	4	5	10	11	8	7	2	.	.	48
32	.	.	3	3	3	4	10	7	1	6	37
33	.	.	1	1	.	4	5	14	8	12	45
34	.	.	.	.	.	.	.	2	12	6	20
35	.	.	.	.	.	.	.	.	4	1	5

As it had already been found that virgins and queens tended to have similar head-widths in each colony, the male data were related to virgin data. This was more easily done and did not involve destruction of the queen or queens. Taking both varieties together a good positive correlation was obtained ($r = + \cdot 8150$, < 1 per cent. P), giving a regression equation of $y = \cdot 4764x + \cdot 445$, y being the expected average male head-width, and x the average virgin head-width. Males as a group had narrower heads than virgins.

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[8] But it should be noted that there is not a fundamental difference here, for the regression relating *macrogyna* queens and workers, if extrapolated towards the origin, passes into a region where queens are smaller than their worker progeny.

(i) *Two Morphological Trends in Queens.*

The largest queens of *macrogyna* (head-widths 39 and 40 divisions) had the dorsal part of their heads dark brown to black in colour: this merged rapidly into orange-brown below at a line level with the eyes. The smallest queens of *microgyna* were less dark on the head, and this changed more gradually to a yellow rather than an orange-brown below. In general, the lighter parts of the bodies of the largest queens were orange-brown and this made the former appear contrasting black and orange and the latter a more uniform dull brown. But no sharp distinction was possible, for a trend closely associated with head-width joined one extreme to the other.

A similar trend in form of ovary was observed: the ovarioles in virgin *microgyna* were typically only two-thirds their length in *macrogyna*. In form they differed as follows: the terminal filament in the largest queens occupied one-third of the length, but in the smallest queens two-fifths, so that the major difference in total ovariole length was due to germarium size. The ovarioles also differed in shape: in *microgyna* they were typically twice as wide in the terminal filament end and only half as wide at the oviduct end as in large *macrogyna* queens. Such differences are probably associated with a smaller fecundity in *microgyna*, which is no doubt compensated by the number of queens in their colonies.

One further anatomical point was noticed: the eyes of queens of both types were approximately the same size, and this made them appear more prominent in the smaller ones.

(j) *Distribution.*

We have found both varieties of *rubra* at Colgrain, Dumbartonshire, and also in Glen Falloch, Perthshire, 25 miles to the north. We have found *microgyna* at Ings, Westmorland, and at Great Barrow, Cheshire.

Certain remarks in the literature make it probable that both varieties have a wide distribution. Thus Donisthorpe (1927, p. 129) states:

> "On April 30th, 1912, I found three small females, partly winged, under a stone, in a colony of *ruginodis* at Hynish, in the Isle of Tiree. S. O. Taylor captured a winged *microgyne* of this species at Wakerley Wood, Northamptonshire, on August 17th, 1915. Wasmann took a number of winged females in a nest of *ruginodis* at Vorarlberg, Feldkirch, in August, 1890, which were smaller than the workers of the same colony."

And later, whilst discussing a colony of *M. laevinodis* var. *ruginodo-laevinodis* Forel found on Lundy Island (*loc. cit.*, p. 124) he says:

> "A small deälated female found in this colony only measures 5·5 mm."

Perhaps a great many colonies of *microgyna* have in the past been relegated to Forel's intermediate category.

3. FURTHER OBSERVATIONS ON *Myrmica laevinodis* Nylander.

Measurement of 192 queen *laevinodis* from 22 colonies collected from Herts, Cheshire and Perthshire gave no evidence of polymorphism. The frequency distribution (Table 14) was symmetrical and unimodal.

TABLE XIV.—*Head-width Frequencies of Queens and Workers of* M. laevinodis *in Micrometer Divisions* (1 *division* = ·03026 *mm.*).

	Head-widths.															Total.
	26.	27.	28.	29.	30.	31.	32.	33.	34.	35.	36.	37.	38.	39.	40.	
Queens .	.	.	.	.	.	.	.	.	.	9	29	63	57	28	6	192
Workers .	2	6	21	44	64	107	158	116	85	28	11	4	.	.	.	646

Mean head-widths : Queens, 37·27 divisions = 1·1278 mm.
Workers, 32·11 „ = 0·9716 „

The mean head-width was very near that of *M. rubra* var. *macrogyna*, 1·1278 mm. (= 37·27 divisions) as compared with 1·1130 mm. (= 36·78 divisions), but the workers averaged smaller, 0·9716 mm. (= 32·11 divisions) as opposed to 1·069 mm. (= 35·34 divisions). They were, in fact, comparable to *microgyna* workers, 1·005 mm. (= 33·2 divisions).

The correlation between the average head-widths of workers, taking a sample of 25 from each of 17 colonies, and the average for queens from the same nest was not very good ($r = +·4976$, $P = 1$–5 per cent.), but the following regression equation was obtained : $y = ·3531x + ·5734$, where y is the average worker head-width, and x the average queen head-width in millimetres. The poorness of this correlation is no doubt due to the fact that most of the colonies were polygynous, and some had over 100 queens.

The frequency distributions of worker head-sizes for 10 randomly selected colonies is shown in Table XV.

TABLE XV.—*Frequency Distributions of Worker Head-widths from* 10 *Colonies of* laevinodis, *in Micrometer Divisions* (1 *division* = ·03026 *mm.*).

Head-widths.	Colony number.									
	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.
26	.	.	.	.	.	2	.	.	.	.
27	.	.	.	2	.	3	.	.	.	.
28	.	1	.	5	.	8	1	1	.	.
29	1	7	1	7	2	3	.	1	.	1
30	3	6	.	6	7	4	3	2	.	3
31	2	8	6	4	6	5	6	.	4	5
32	9	2	9	1	9	.	5	7	12	6
33	3	1	2	.	1	.	6	5	6	5
34	5	.	4	.	.	.	4	6	3	3
35	2	.	2	.	.	.	.	1	.	2
36	.	.	1	.	.	.	.	.	.	.
37	.	.	.	.	.	.	.	2	.	.

The variability is comparable with that of both types of *rubra*. In aggregate this data forms a symmetrical unimodal frequency distribution (see

Table XIV)[9]. *Laevinodis* thus appears to combine in a single form—the macrogyne—characters which, in *rubra*, are divided between two forms.

4. DISCUSSION.

In this paper we have presented evidence to show that *rubra* is an incompletely dimorphic species. A case in plants which is perhaps analogous, has been described: the Lesser Celandine (*Ranunculus ficaria* Linn.) occurs in two forms, one setting viable seed and the other reproducing vegetatively by means of tubercles (Marsden-Jones, 1935; Metcalfe, 1938 and 1939). In ants, Gösswald (1942) has shown that *Formica rufa* L. consists of several races, some of which differ in ways similar to those just described in *Myrmica rubra*. *F. rufa rufa* is equivalent to *M. rubra* var. *macrogyna*, as it has monogynous colonies, and queens with long ovarioles which lay many eggs; the queens found colonies by entering nests of *Formica fusca* L. *F. rufa rufo-pratensis minor* is equivalent to *M. rubra* var. *microgyna*, for it exists in polygynous, polydomous colonies, and has queens that are relatively small (though not as small as their workers), with short ovarioles and low fecundity. *F. rufa rufo-pratensis major* has intermediate characters. Talbot (1948), has recently found that two varieties of another species of *Formica* differ, amongst other ways, in whether they are monogynous or polygynous. *Formica pallidefulva nitidiventris* Emery was monogynous in all of 24 nests examined and recorded, whereas *F. pallidefulva schaufussi incerta* Emery was frequently polygynous, and Talbot suggests that secondary pleometrose and colony fission occurred. In this case microgyny was not involved, but Holliday (1903) has recorded microgynes of the former variety.

In the area from which our colonies of *M. rubra* have been collected, *macrogyna* has predominated in transitory habitats, and those which have only been suitable for ant colonization for a short time (e.g. in seral and mosaic cyclic vegetation types) whereas *microgyna* has been found in comparatively stable areas. Gösswald lists a wider range of habitat occurrences for the monogynous form of *F. rufa*. than for the polygynous form, and comments that the latter lives in especially favourable ant sites. In both these cases two possibilities appear to exist: either that the polygynous form is gradually derived from the monogynous in each habitat that persists for long enough in a favourable condition, or that each species is developing (or has developed), in an evolutionary sense, varieties adapted to temporary and stable habitats respectively; hybridization of these may still occur. Such problems are being investigated.

Wheeler (1937) has reviewed the subject of microgynes, and pointed out that these females occur as "occasional anomalies," or "complemental females," in a wide variety of ants. Donisthorpe (1927, p. 122) recorded an instance of a microgyne *laevinodis*, which was sole queen in a nest, and Reichensperger (1911) has recorded two similar cases in *Plagiolepis pygmaea* Latreille which he regarded as successfully established mutants. In the subgenus *Microgyna* of the genus *Formica* the only known females are microgynes. *M. rubra* appears to lie between these extremes.

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[9] This is also the case with *rubra*, if workers of the two varieties are pooled and considered together.

5. Summary.

1. A biometrical study of the similar species, *Myrmica laevinodis* Nylander and *Myrmica rubra* L., has shown within the limits of the material available, that colonies of one species can be distinguished from colonies of the other, and that, as a result, Forel's intermediate category, *Myrmica laevinodis* var. *ruginodo-laevinodis*, will probably disappear. A certain number of individual workers of each species were indistinguishable.

2. *M. rubra* has been shown to exist in two varieties, occurring together in various localities, and both probably widespread, showing a gradual transition of morphological characters and a more abrupt transition of ant-perceptible characters. Each variety differs primarily in its propagation methods: the one having the primitive method of dissemination of fecundated queens which may found colonies alone or in aggregate; the other, receiving queens after nuptials back into their nests, being highly polygynous as a result, and reproducing by fission of polydomous societies. The former variety is macrogynous, and the latter microgynous. New names are introduced for these varieties.

3. *M. laevinodis* gave no evidence of polymorphism, and appears to combine in a single form—the macrogyne—the characters divided between two forms of *rubra*.

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CONTENTS

SATCHELL, G. H., B.Sc., Ph.D. The early stages of the British species of *Pericoma* Walker. (Diptera: PSYCHODIDAE.) . . 411–447, 26 figs.

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THE EARLY STAGES OF THE BRITISH SPECIES OF *PERICOMA* WALKER. (DIPTERA : PSYCHODIDAE.)

By G. H. SATCHELL, B.Sc., Ph.D.
(*Department of Zoology, Otago University, Dunedin.*)

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(Read 1st June, 1949).

With 26 Text-figures.

INTRODUCTION.

THE larvae and pupae of the genus *Pericoma* Walker are common objects amongst clumps of damp moss and algal mats bordering the margins of streams in Britain. They are sometimes exceedingly abundant, and several species may be taken within a few yards of each other. The genus is a large one, and twenty-four species are mentioned in the British list (Tonnoir, 1940), but our knowledge of its early stages is very incomplete. Walker (1856) has given a brief description of the larva of *P.* (*Ulomyia*) *hirta* L. = *fuliginosa* Meigen, from which it is clear that he was dealing with the larva of some other species. Miall (1895) has given a full account of the larva and pupa of *P. neglecta* Eaton, under the name *P. canescens* Meigen, and his mistake has been incorporated into the papers of subsequent workers (Grünberg, 1910; Feuerborn, 1913). Thienemann (1909) has described the naked-eye appearance of the larva of *P. cognata* Eaton under the name of *P. nubila* Eaton. Feuerborn (1923), in a paper which represents quite the most important contribution to our knowledge of the structure and ecology of larvae of this genus, has described and figured the larvae of *P. canescens*, *P. neglecta*, *P. cognata*, *P. pulchra* Eaton, *P. calcilega* Feuerborn, and *P. fusca* Macquart. This paper was not intended, however, to be a taxonomic study, and no formal description of the larvae of the species was given. Only such features were mentioned as appeared to be adaptations to marginal life, and in the case of *P. canescens* and *P. fusca*, only portions of the larvae were figured. His descriptions cannot, therefore, be regarded as satisfactory accounts of the species.

With a view to filling this gap in our knowledge of the early stages of the PSYCHODIDAE, the writer has been collecting and breeding out *Pericoma* larvae for the last three years. Absence from Britain now prevents the completion of the work, and it has been decided to publish the descriptions of the early stages of the twelve species that have so far been obtained. By incorporating three of Feuerborn's descriptions, a key can be constructed covering fifteen of the twenty-four British species. In addition, short notes on the habitats in which the species have been found will be given after the description of each.

Tonnoir (1940) divided the genus into three groups on characters of wing shape and venation. In group 1, containing the species *P. trifasciata* Meigen, *P. calcilega* Feuerborn, *P. blandula* Eaton, *P. pulchra* Eaton, *P. exquisita* Eaton, *P. pseudexquisita* Tonnoir, *P. diversa* Tonnoir, *P. fallax* Eaton and *P. avicularia* Tonnoir, the larvae and pupae of all but the second and last have been obtained and full descriptions can be given. The larva of *P. calcilega* has been described and figured by Feuerborn (1923) sufficiently fully to be included in the key. In group 2, containing the species *P. trivialis* Eaton, *P. nubila* Eaton, *P. palustris* Eaton, *P. gracilis* Eaton, *P. mutua* Eaton, *P. cognata*, *P. compta* Eaton, *P. extricata* Eaton, *P. pilularia* Tonnoir, *P. hibernica* Tonnoir, *P. canescens* and *P. neglecta*, the larvae and pupae of the first two and the last have been obtained, and Feuerborn's (1923) description of *P. canescens* and *P. cognata* can be included in the key. In group 3, containing the species *P. fusca* Macquart, *P. auriculata* Walker and *P.* (*Ulomyia*) *fuliginosa*, material of the first and last has been obtained and will be described. Of the fifteen species of larvae dealt with in this paper, nine are thus described for the first time, three are amplifications of previous descriptions, and three are inclusions from Feuerborn's accounts.

MATERIAL AND METHODS.

All larvae and pupae described in this paper have been identified by breeding collected material through to the adult. The larval and pupal exuviae are remarkably resistant structures and can be treated with potash, glacial acetic acid and clove oil, mounted on strips of celluloid and included on the pin of their appropriate adult. In this way the possibility of confusing material is reduced to a minimum, since the larva, pupa and adult used in the description, are all the product of a single individual.

Pericoma larvae survive quite well in small glass dishes containing moss or decaying leaves. Each larva was given a separate dish, and when it pupated the pupa was removed to a capsule containing moistened filter paper, given a temporary code number, and the same number copied onto the celluloid strip bearing the larval exuviae. With the isolated exception of *P. trivialis*, the writer has been unable to get the adult flies to deposit their eggs in captivity, so it has not been possible to prepare cultures of each species, as was done with flies of the genus *Psychoda*. *P. trivialis* once deposited its eggs when confined over pledgets of cotton wool soaked in ditch water. The larvae hatching from these grew to maturity in a four-ounce jar containing saturated cotton wool mixed with scalded horse dung.

Pericoma larvae are heavily pigmented, and as identification involves the inspection of both dorsal and ventral surfaces, it is essential to get them thoroughly cleared. Immersion in cold 5 per cent. caustic potash for two days, followed by a day each in glacial acetic acid and clove oil, gives a well-relaxed specimen in which a good deal of the black pigment has been dispersed. Pupae should be treated similarly, as pigment on the wall of the respiratory horn obscures the felt chamber within, on the shape of which identification often depends; they should be mounted dorsal side uppermost. The larvae of two British species, *P. trifasciata* and *P. calcilega*, are normally thickly incrusted with lime when collected, and the specimens are spoilt by the violent effervescence which results in glacial acetic acid. Such larvae should be left for a night in 1 per cent. acetic acid before being put into caustic potash.

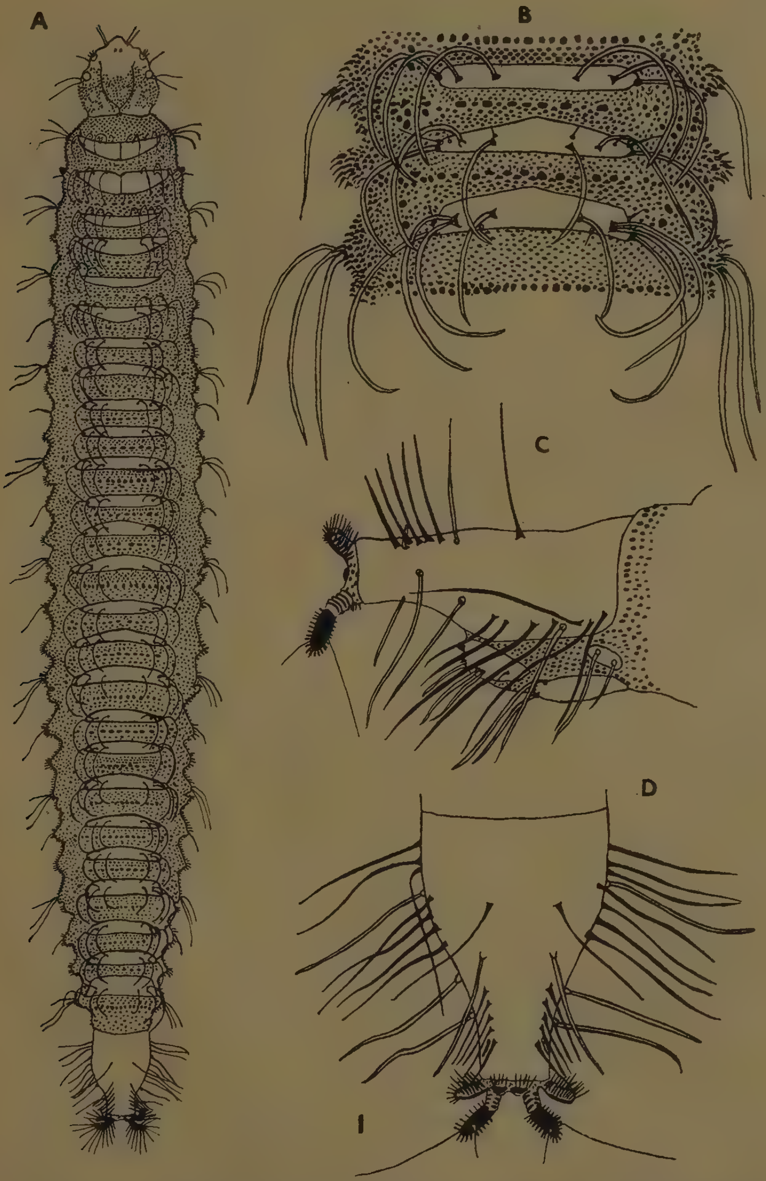

FIG. 1.—Larva of *P. trivialis* Eaton. A, Whole larva, × 24 ; B, fourth abdominal segment, × 92 ; C, siphon, lateral view, × 76 ; D, siphon, dorsal view, × 76. Throughout the illustrations siphonal accessory setae have been represented solid, and siphonal true setae in outline.

THE GENERAL STRUCTURE OF A *Pericoma* LARVA.

The identification of *Pericoma* larvae involves some acquaintance with the chaetotaxy, particularly of the abdominal segments, and a knowledge of the structure of the siphon, in this genus.

The larva has a well-developed head and eleven evident body segments. The head is usually oval in outline, though occasionally markedly triangular, and has a U-shaped epicranial suture. Ventrally, the mouthparts lie in a semicircular depression bounded posteriorly by the toothed mentum. The mandible, maxilla and labrum are similar to those of *Psychoda albipennis* Zetterstedt (Keilin and Tate, 1937). The antennae are borne laterally, and each consists of two short rods, a longer rod, and a hair (fig. 3E). The head capsule is covered by a pattern of small circular denticles, and this pattern is remarkably constant. Centrally are paired posterior clear areas, and anterior to these are one or two medial ones (fig. 4C). Immediately lateral to each epicranial suture is a large, elongate, clear area, and two circular ones occur lateral to this. On the side of the head near to the antenna lies a raised patch of transparent cuticle, the ocellus, and behind this is another clear area. A varying extent of the anterior region of the head is free from these denticles.

All segments except the terminal one are divided into ring-like subsegments or annuli. There are two of these in each of the three thoracic and first abdominal segments, and three in each of the remaining six abdominal segments. Each annulus bears a rectangular sclerotized plate dorsally, termed the tergal plate, and there are thus twenty-six of these in all. There is no tendency for the anterior plates of the series to be missing, as was the case in some of the larvae of the genus *Psychoda* (Satchell, 1947), and all *Pericoma* larvae so far examined have a full set. There is a great variety, however, in the length and arrangement of the setae on the tergal plates, and Feuerborn (1927) has worked out the chaetotaxy of the larva. He points out that a distinction has to be drawn between true setae, which are articulated structures with a basal ring, and are presumably sensory in function, and accessory setae which are simple extensions of the cuticle. Accessory setae are of sporadic occurrence, being absent in some species and very numerous in others. They are not even constant in their occurrence within the species in some of the very setose forms, such as *P. trivialis*. True setae, on the other hand, though they may be reduced in size, are rarely absent, and the same setal plan can be made out in all the species so far examined. In the descriptions which follow the number of setae stated refers to that of one half of the structure, as the larvae are perfectly bilaterally symmetrical.

The setae present on the abdominal segments will be described first as they are of greatest importance as sources of diagnostic characters. Those present on the dorsal surface will be referred to as the pro-, meso- or metatergal setae, according as to whether they occur on the fore, mid or hind plate. The very minute intertergal setae, figured by Feuerborn (1927), are invisible except in specially prepared portions of isolated cuticle, and need not be considered. There are no true setae on the protergum (fig. 1B), but two or three large accessory setae occur here in some species. There are always three minute true setae on the mesotergum, and in setose species three large accessory setae as well. In species with the setae reduced only the three minute true ones are present. On the metatergum all are true setae, with four large and two small ones in each half-plate. The most medially placed of each side is separated from its partner by a distance termed by Feuerborn (1926) the "Mittelraum." Its relation to the width of the plate as a whole is a useful diagnostic character, and indicates the extent to which the setae have shifted towards the lateral margins ; this distance will be referred to as the intersetal space. Lateral to the medial seta are two with their bases approximated, and lateral to these is a fourth, on the margin of the plate. These four setae are always larger than the remaining two small ones, one of which lies immediately anterior to the fourth, also on the margin, and the other between the medial and the paired setae. As all the metatergal setae are true setae they are present in all species, though they tend to be smaller in the species with reduced setation. In the descriptions that follow, the setae will be numbered from the centre outwards, and when two setae have their bases approximated their numbers will be bracketed together.

Each abdominal segment bears setae on the lateral margin. On the posterior annulus two long and one short true setae occur, whilst a single true seta occurs on the anterior annulus. Ventrally, each middle annulus bears two setae ; around their bases are small sclerotized plates, and in some species the two plates of each side are joined. On the posterior annulus are two setae with their bases touching ; sometimes one of these setae is much lengthened and strongly hooked at the tip.

The chaetotaxy of the thorax differs from that of the abdomen, and that of the prothorax differs from that of the meso- and metathorax. The setae on the thoracic terga are borne on the anterior margin, whilst in the abdominal segments they are borne on the posterior margin. Unless otherwise stated all the thoracic setae mentioned are true setae. On the prothoracic protergum a row of seven setae occurs, which are not of equal length, and are arranged as follows : Short, long, short, long, short (long, long). On the metatergum the most medial seta is long, and a short one occurs lateral to it. More laterally lies a pair of long setae whilst on the margin are two setae, one long, one short, with their bases touching. The proterga of the meso- and metathorax show various arrangements, but there are never more than three true setae in each. Sometimes all three are long ; sometimes two are long, one is short, and near it is a long accessory seta. On the metaterga, there is usually a single seta medially, and two pairs, more laterally, the outer pair being on the lateral margin. Immediately anterior to it, lies a small seta, whilst an additional small one lies between the most medial seta and the first pair. The setae on the lateral margins of the thorax are located on the anterior annuli only. On each lies a group of two small and two long ones. Ventrally, lies a group of setae termed by Feuerborn (1927) the "pedichaeten." Each group is supposed to represent the sensory vestiges of the thoracic legs, and consists of two large and four small setae. A seta occurs on each side of this group whilst two more occur in the anterior annulus.

On the posterior annulus of the prothorax lies the anterior spiracle elevated on a protuberance. There is not the variety of form seen in the anterior spiracles of *Pericoma* larvae such as occurred in those of *Psychoda*. In all it consists of a cylindrical sclerotized structure with a terminal opening partly occluded by a plug with radiating threads connecting it to the rim.

The terminal segment (figs. 1c and 4c) is a compound structure derived from portions of segments 8, 9 and 10, and bears the tubular respiratory siphon with the posterior spiracles at the apex. The siphon has been formed from a sclerotized plate, termed the dorsal plate, which proximally covers the dorsal and most of the lateral surfaces of the terminal segment, and, distally, has been rolled up to form a tube. The length of the dorsal plate of the siphon is a convenient standard against which to measure other siphonal structures, and is to be taken as the distance, in the mid-line, from the anterior margin, where sclerotization commences, to the posterior margin. Laterally are three large and one smaller true setae, whilst two small true setae occur dorsally. Various accessory setae are borne on the siphon, and are of great diagnostic importance. Mid-ventrally, lies a large median plate, the preanal plate, with two setae on each side of its posterior margin ; behind the preanal plate is the anus. Above this are paired adanal plates with three long and one short setae. More anteriorly, on the lateral area of cuticle between the dorsal and preanal plates, are small rectangular lateral plates. Each bears a long and a short seta.

The posterior spiracles are protected by two pairs of processes fringed with long hairs. These are accessory setae, and serve to entrap a bubble of air should the larva be submerged. The ventral processes are always the longer, and each bears four true setae near the tip ; a short one dorsally, a long and a short one ventrally and a long one laterally. These tend to be obscured by the long, hairy fringe. There is a single, short, true seta on the dorsal process. Each process is heavily sclerotized, and annular sclerotized elements are present around the base. When mention of the length of the process is made, it is to be taken as including these annular sclerotizations. Between the bases of the dorsal and ventral processes of each side, lies a spiracle, consisting of a central plug with radiating threads connecting it to the spiracle rim. Around the spiracle, and between the bases of the processes, are numerous polygonal sclerotizations. Between the margin of each spiracle and the posterior margin of the dorsal plate, these polygonal elements are produced into long hairs which overlie the dorsal plate. Martini (1928) interprets the spiracles as being intersegmental in position, lying on the boundary between the 8th and 9th segments. The dorsal plate, lateral plates and dorsal processes have all been derived from the 8th segment, the ventral processes and adanal plates from the 9th and the preanal plate from the 10th.

The body wall is covered with a vestiture of numerous sclerotized thorns which show regional differences. In between the tergal plates they are usually very small and arranged in regular rows, whilst on the intersegmental lines they are very large and without points. Two large elements occur opposite the lateral margin of each metatergum, and one opposite the margin of each protergum. In some species larger elements are also present interannularly. A row of pointed or comb-like elements is often present on the ventral surface of the abdominal annuli ; these will be referred to as the ambulatory elements.

THE GENERAL STRUCTURE OF THE PUPA.

The pupae are less easy to identify as they have fewer structures which show any differentiation amongst the species. The best sources of diagnostic

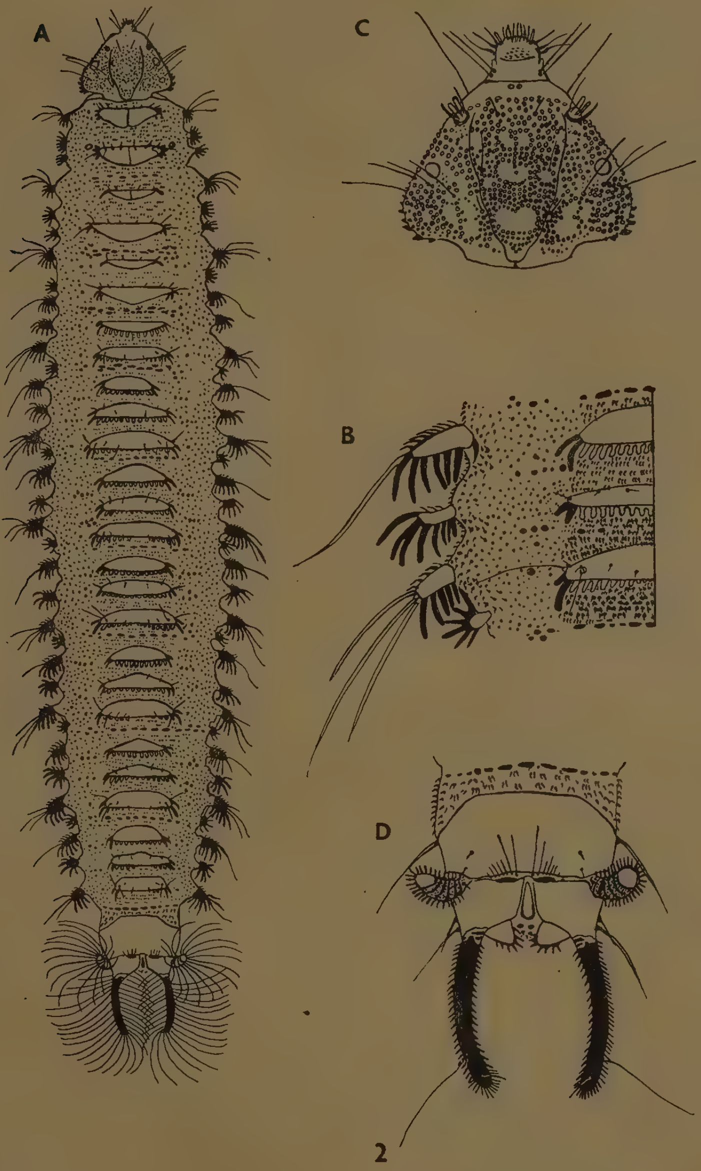

FIG. 2.—Larva of *P. pulchra* Eaton. A, Whole larva, × 34 ; B, Fourth abdominal segment, × 80 ; C, Head, × 92 ; D, Siphon, dorsal view, × 76.

characters are the respiratory horns, the fringes of cuticular points and sensillae on the abdominal segments and the dorsal teeth of the terminal segments.

The respiratory horns of all species are fundamentally similar to that of *Psychoda alternata* Say (Satchell, 1948*b*). Each consists of an inner tube, the felt chamber (fig. 16) which meets the outer covering at a number of thin circular areas, the pits. These, primitively, are borne on the apex and posterior surface of the horn and form a double row. Where the wall of the horn is some distance from that of the felt chamber the latter is connected to the pits by a number of thin transparent tubes. The felt chamber passes through the annulated base, to the tracheal extension, and at the junction of the two is the darkly-pigmented lever which forms part of the mechanism, described in detail, in the pupa of *Psychoda*. This mechanism, it was suggested, may be a closing mechanism, and similar structures occur in all the *Pericoma* pupae so far examined. When measurements of the horn are given, the width is to be taken half-way up and the length from the most distal annulation.

The fringes on the ventral surface of the abdominal segments are not so distinct, in the different species, as are those of the dorsal surface. Hence, in the descriptions, when mention is made of the abdominal fringes, reference to the posterior fringe on the dorsal surface of the seventh abdominal segment should be made. Similarly, in the terminal segment, which has paired dorsal and ventral teeth, it is only the dorsal teeth which show much differentiation amongst the species. Usually each consists of a strong, pointed outgrowth of cuticle, with three trichoid sensillae distributed somewhere around its base. Often, however, one of these trichoid sensillae has its hair-like element replaced by a strong point, shaped like an awl, and this modified sensilla takes the place of the cuticular tooth. Sometimes an intermediate condition prevails, and the awl-like sensilla is mounted half-way up the side of the cuticular point, so that the dorsal teeth appear bifid.

The species *P. trivialis*, *P. nubila*, *P. fuliginosa* and *P. neglecta* all have the respiratory horn in the primitive condition, with the felt chamber undivided and the pit row confined to the upper third of the horn; it is impossible to distinguish these pupae from one another unless reference is made to the abdominal fringes. This type of horn also occurs in the genus *Telmatoscopus* Eaton, for Feuerborn (1926) has figured the respiratory horns of *T. ustulatus* Walker and *T. similis* Tonnoir, and they appear to be indistinguishable from those of the four species of *Pericoma* previously mentioned.

Key to Larvae.

1. Larvae with ten setae, or more, on lateral margin of siphon, as in fig. 1c and d . . . . 2.
   With four setae or fewer on lateral margin of siphon as in fig. 4c and d 4.
2. No more than three long setae on proterga, three on mesoterga, and four on metaterga, of abdominal segments . . . . 3.
   Four long setae on proterga, six on mesoterga, and six on metaterga of abdominal segments . . . . *P. cognata* Eaton.
3. Setae of abdominal tergal plates grouped closely together at plate lateral margins; mounted on prominent sclerotized bosses; inter-setal space half plate width or more . . . . *P. canescens* Meigen.

Setae of tergal plates well spaced so intersetal space is one-third plate width; not mounted on sclerotized bosses; posterior lateral setal group of abdominal segments consisting of three hairs of almost equal length; a row of five or six accessory setae on dorsal surface of posterior third of siphon; ventral siphonal processes angulated *P. trivialis* Eaton; *P. nubila* Eaton.

4. Head markedly triangular in outline, broadest at, or immediately anterior to, the base (as in fig. 2c) . . . . 5.

Head quadrate or oval in outline, broadest immediately posterior to the middle (as in figs. 10c and 11c) . . . . 7.

5. Larvae coated with a thick crust of lime; tergal setae broad and shaped like scythe blades . . . . 6.

Larva without lime covering; much flattened dorso-ventrally; tergal setae reduced; each annulus laterally produced into a sclerotized process bearing a posterior fringe of prominent teeth; ventral siphonal process forming quadrate plates at their bases; more than twice as long as dorsal plate of siphon (fig. 2) . . *P. pulchra* Eaton.

6. Abdominal proterga with one large and three smaller flattened setae; mesoterga with one large and five smaller flattened setae; siphon dorsal plate with one large and three smaller flattened setae *P. calcilega* Feuerborn.

Abdominal proterga with three equal-sized flattened setae; mesoterga also with three; siphon dorsal plate with one large and two small flattened setae (fig. 3) . . . . *P. trifasciata* Meigen.

7. Larvae with tergal setae strongly developed; two setae on abdominal proterga . . . . 8.

Larvae with tergal setae weakly developed; no setae on abdominal proterga . . . . 13.

8. Two setae on each side of ventral surface of middle annulus of each abdominal segment, with their bases joined by a sclerotized plate; ventral processes very long, four-fifths length of dorsal plate; paired setae of posterior abdominal annuli unhooked (fig. 4) *P. neglecta* Eaton.

Two setae on each middle abdominal annulus with separate sclerotized plates around their bases . . . . 9.

9. Preanal plate divided transversely into two halves; three equal mesotergal setae; intersetal space one-third plate width, ventral processes slightly more than half dorsal plate (fig. 6) *P. exquisita* Eaton.

Preanal plate undivided; either two long and one shorter mesotergal setae, or only two . . . . 10.

10. Ventral processes of siphon nine-tenths length of dorsal plate; paired curved setae of preanal plate subequal with their bases almost touching; posterior margin of preanal plate with numerous black sclerotized tubercles; mesotergal 3 one-quarter length of mesotergal 2 (fig. 5) . . . . *P. diversa* Tonnoir.

Ventral processes less than half length of dorsal plate; preanal plate setae either unequal or, if approximately equal, then they are separated by a distance three to four times the width of one seta base . . . . 11.

11. Inner seta of preanal plate enormously longer than outer seta, very strongly curved; outer seta short and fringed; intersetal space one-third plate width; mesotergal 3 one-third length of mesotergal 2 (fig. 7) . . . . *P. fallax* Eaton.

Preanal plate setae of approximately equal length . . . . 12.

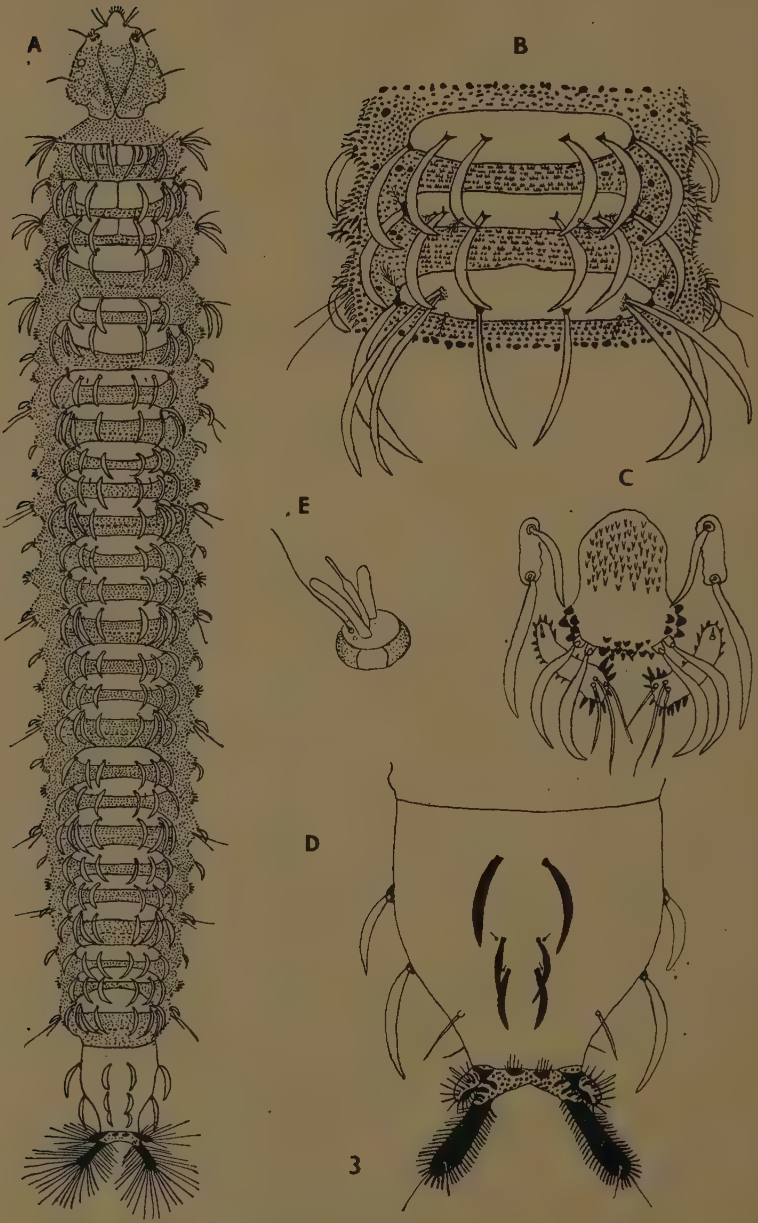

Fig. 3.—Larva of *P. trifasciata* Meigen. A, Whole larva, × 45; B, Fourth abdomina segment, × 117; C, Preanal plate, × 166; D, Siphon, dorsal view, × 166; E, Antenna, × 427.

12. Intersetal space less than half plate width ; mesotergal 3 one-third to one-half length of mesotergal 2 ; outer seta of pair on ventral surface of each posterior abdominal annulus hooked at tip ; preanal setae strongly curved (fig. 8) . . . . *P. blandula* Eaton.

Intersetal space one-half to seven-tenths plate width ; mesotergal 3 absent, so only two setae on mesoterga ; ventral posterior annular setae not hooked ; preanal setae not obviously curved (fig. 9) *P. pseudexquisita* Tonnoir.

13. Larva whitish coloured ; head markedly quadrate ; surface free from denticles ; siphon long and slender with tapering terminal portion twice as long as swollen basal region ; ventral mid-annular setae united by a sclerotized plate (fig. 10) . . . . . . *P. fusca* Macquart.

Larva intensely black ; head oval, covered in posterior part with numerous denticles ; siphon not long, with tapering terminal portion scarcely as long as basal part ; ventral mid-annular setae with separate sclerotized plates (fig. 11) . . *P.* (*Ulomyia*) *fuliginosa* Meigen.

Key to Pupae.

1. Only primary pits on respiratory horn, appearing as a simple double row of circular patches of lighter cuticle . . . . 2.

Each primary pit connected laterally to one or more secondary pits, so that pairs or ribbons of pits are formed . . . . 8.

2. Pits arranged in a circle around apex of horn, connecting by radiating tubes to swollen end of felt chamber which bears a delicate reticulate meshwork on its wall ; horn folding into a depression on sides of thorax ; abdominal segments with a fringe of teeth on lateral margins ; dorsal teeth of terminal segment absent (fig. 12) *P. pulchra.*

Not such pupae . . . . 3.

3. Horn cylindrical, five to six times as long as broad, with a delicate reticulate meshwork on felt chamber wall (fig. 13) ; sensillae of posterior dorsal abdominal fringes trichoid (fig. 24) ; dorsal teeth of terminal segment replaced by a single, median, bifid, strongly rugose, spade-like process . . . . *P. fusca.*

Horn cylindrical, lacking reticulations on felt chamber ; paired dorsal teeth on terminal segment . . . . 4.

4. Pit row dividing apically into a long and a short row (fig. 14) ; sensillae of posterior dorsal abdominal fringes in form of long-bladed awls (fig. 25) ; each dorsal tooth of terminal segment appearing bifid, consisting of one awl-like sensilla and a cuticular point of equal length . . . . *P. diversa.*

Pit row not divided apically into two . . . . 5.

5. Felt chamber with a subapical constriction immediately prior to where it begins to meet pit-bearing area (fig. 15) ; sensillae of posterior dorsal fringe in form of short-bladed awls (fig. 26) ; dorsal teeth of terminal segment consisting of an awl-like sensilla with a small cuticular point at the side . . . . *P. trifasciata.*

No subapical constriction to felt chamber . . . . 6.

6. Posterior dorsal fringe of seventh abdominal segment with sensillae awl-like (fig. 22) ; dorsal teeth of terminal segment formed from short-bladed, awl-like sensillae . . . . *P. neglecta.*

Posterior fringe with trichoid sensillae . . . . 7.

7. Medial trichoid sensillae of posterior dorsal fringe of seventh abdominal segment widely separated; no cuticular teeth between (fig. 21) . . . . *P. fuliginosa.*
Medial trichoid sensillae close together with about three cuticular teeth between (fig. 23); prominent incurved cuticular teeth on dorsal surface of terminal segment . . . . *P. trivialis; P. nubila.*
8. From each primary pit, one secondary pit is given off, so horn is covered with pits arranged in pairs; felt chamber at least three-branched . . . . 9.
From each primary pit a ribbon of between three and seven secondary pits is given off; felt chamber either unbranched or two-branched 10.
9. Horn at least three times as long as broad; up to one hundred pairs of primary pits (fig. 17) . . . . *P. exquisita.*
Horn not more than twice as long as broad; between fifty and sixty pairs of primary pits (fig. 18) . . . . *P. blandula.*
10. Felt chamber either unbranched, or at most a branch much shorter than the remaining portion is given off half-way up (fig. 19) *P. pseudexquisita.*
Felt chamber dividing half-way up into two equal branches (fig. 20) *P. fallax.*

P. trivialis Eaton.

Larva.—Fig. 1A. 7–9 mm. long; normally thickly covered with mud and detritus; covering tending to be divided into two ridges with gutter down middle, corresponding to lateral setal groups on tergal plates. Head oval, broadest just behind middle; denticles reaching beyond ocelli, forming a row of 10 or more small teeth when viewed in outline on head lateral margin; mentum with 13–15 bluntly-pointed teeth. All setae very long; prothoracic chaetotaxy on conventional plan; mesothorax with protergal 1 small, 2 and 3 long; a long accessory seta occurring between 1 and 2, and another between 2 and 3, making a row of five in each half-plate; metatergum with an additional seta medially, otherwise on conventional plan; abdominal segments (fig. 1B) with tergal plates rather more than half body width; protergum with three long setae, chaetotaxy otherwise on conventional plan; all setae strongly curved posteriorly, subequal, reaching beyond margin of next tergal plate; setae well spaced, so intersetal space is only one-third plate width; lateral group on posterior annulus consisting of three setae of almost equal length; ventral mid-annular setae with separate sclerotized plates around bases, the outer plate larger than the inner; lateral margins of segment deeply incised between annuli. Siphon (figs. 1C and D), somewhat variable in shape; terminal processes short; ventral pair bent at point where solid sclerotization is replaced by annular thickenings; one-seventh length of dorsal plate of siphon; dorsal process two-thirds length of ventral; hairy fringes not well developed. Lateral margin of siphon bearing, in addition to the four true setae, a variable number, between six and ten accessory setae, which combine to give the appearance of a hairy fringe; dorsally, in addition to the two true setae, one of which is greatly elongated, there are five or six accessory setae, in posterior third of siphon; preanal plate with posterior setae weak, equally spaced, a fringe of comb-like elements between them. Vestitural elements almost devoid of teeth on dorsal surface of larva; with long, hairy fringes laterally; larger elements interannularly as well as intersegmentally; ambulatory elements forming combs with long, hairy fringes; most pronounced on anterior annulus of each abdominal segment.

Pupa.—Respiratory horn very similar to that of *P. neglecta* (fig. 16). Distinguished by posterior fringe of dorsal surface of seventh abdominal segment which has two or three points between medial sensillae (fig. 23); sensilla element trichoid, mounted on side of

a pointed tooth ; more lateral paired sensillae both trichoid. Dorsal teeth of terminal segment formed from sclerotized, pointed outgrowths of cuticle ; three trichoid sensillae around base of each, no sensilla at tip.

The larva and pupa of this species are indistinguishable from those of the closely-related *P. nubila.* These two species are separated only by the presence of a tuft of white hairs on the frons, and white scales on the antenna, of the male of *P. nubila*, and Tonnoir (1940) suggests that they may be a single species with dimorphic males, as he found a good many intermediates in Feuerborn's collection. This suggestion is certainly borne out by an examination of their larvae and pupae. The problem of these geminate species in the PSYCHODIDAE is a difficult one, however, since in another pair, *P. canescens–P. neglecta* the larvae differ considerably. In a family in which so many of the species are separable only on characters present in the male, the idea of dimorphic males is one which cannot be accepted until the early stages of many more of these geminate species have been described.

The larva of *P. trivialis* is very variable, both in the shape of the siphon, and in the number of accessory setae on it. It is exceedingly common and has been collected from every locality that has been visited regularly. It was abundant on the stony margins of a stream in Rutland, creeping about in the mud film. It was one of a number of Psychodid flies breeding out from mud collected from a mud flat at Meanwood Valley, near Leeds. It had colonized the mixture of mud and decaying leaves in a drying fish-pond in Nottinghamshire. All these localities had in common the presence of mud rich in organic remains and the absence of swiftly-flowing water. Its ubiquity is due to the fact that such conditions are to be found on the margins of the majority of streams. The larvae crawl about on the surface fully exposed to view, but the covering of mud held by the dorsal setae make them very inconspicuous, and they are often first recognized by the winding trails they leave on the glistening mud film.

As has already been stated, this is the only species which the writer has succeeded in rearing in culture, where it grew to maturity on a diet of scalded horse dung. The material from which the descriptions in this paper were derived consisted of larval and pupal exuviae of adult male *P. trivialis.*

Both *P. trivialis* and *P. nubila* belong in Tonnoir's second group, and it is in this group that most of the species whose larvae are as yet unknown occur. Feuerborn (1923) mentions that he has found a number of species of larvae which have a detritus covering, and are much alike, so the possibility exists that when these, at present unknown, larvae are described, the account of *P. trivialis* given here will have to be augmented. The problem is complicated by the fact that there is no generic character separating the larvae of the genus *Telmatoscopus* Eaton, of which there are twenty-three British species, from those of *Pericoma*. *T. ustulatus* Walker has a larva very like that of *P. trivialis*, differing only in having two large teeth on the head lateral margin (Feuerborn, 1926), so the possibility that there are a number of larvae in this genus with a close resemblance to *P. trivialis* has to be borne in mind.

P. cognata Eaton.

No material of this species has been collected by the author, but Feuerborn (1923) gives a figure of the larva. From this it can be seen that the tergal

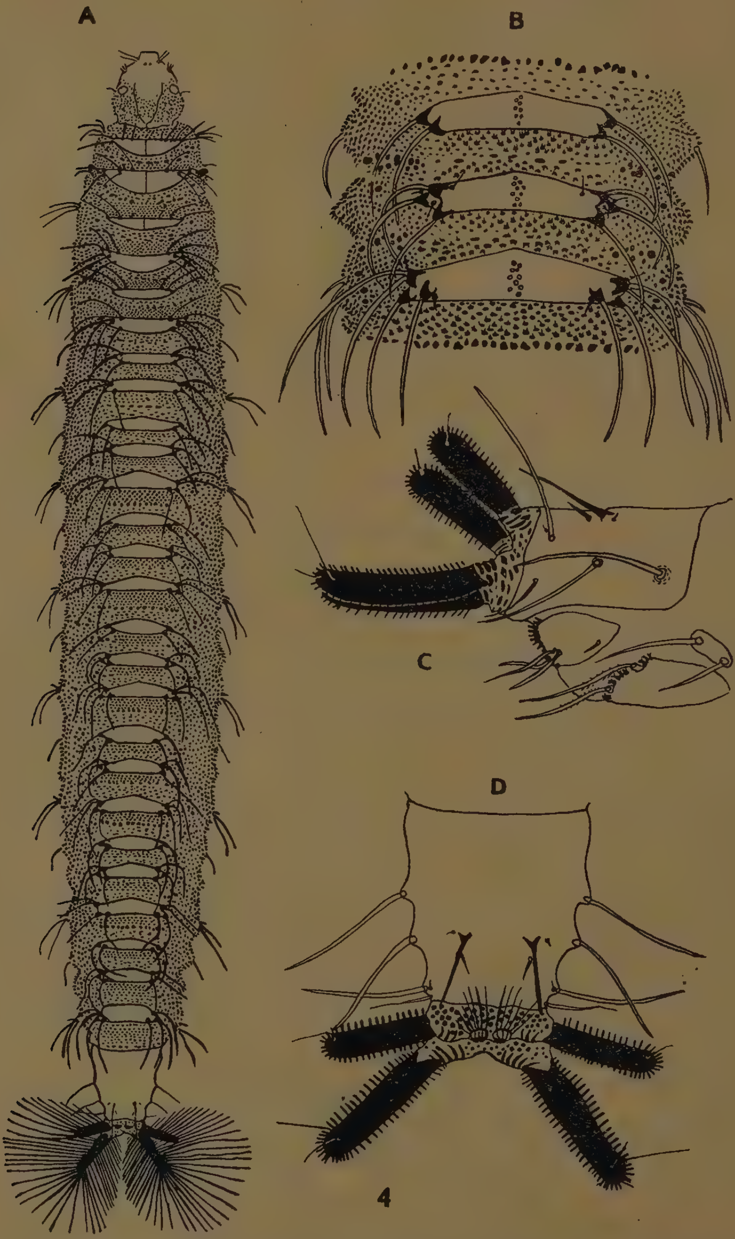

Fig. 4.—Larva of *P. neglecta* Eaton. A, Whole larva, × 20; B, Fourth abdominal segment, × 76; C, Siphon, lateral view, × 76; D, Siphon, dorsal view, × 76.

setae are extremely well developed, there being four long protergal setae, six long mesotergal setae and six long metatergal setae in each half-plate. It is stated to carry a thick covering of mud, and, like the other detritus-covered species, has a number of accessory setae on the lateral margin of the siphon. Thienemann (1909) has described the habitat of this species, under the name of *P. nubila*, as damp rocks on mountain road sides, where water flows, making loamy fissures on the rock surface. Feuerborn (1923) pointed out Thienemann's error in identification.

P. pulchra Eaton.

The larva of this species was figured by Feuerborn (1923), and a more detailed account of the thoracic segments was included in his paper on chaetotaxy (1927). It is so strongly modified to a life on the undersides of stones in moderately swift streams that it stands apart from all the other species.

Larva.—Fig. 2A. 4–5 mm. long, normally free from detritus, strongly flattened dorso-ventrally; blackish. Head (fig. 2C) markedly triangular, broadest just anterior to base; ocelli more posterior than usual; denticles very numerous, carried far forward to a line anterior to insertion of antennae; forming conspicuous teeth on lateral head margin; mentum with a single median tooth. Body bearing strongly sclerotized processes laterally on each annulus, an additional process present immediately behind each posterior annulus, so each thoracic segment bears three processes and each abdominal four; each process with a fringe of strongly sclerotized teeth. Thoracic tergal plates with groups of sclerotized teeth at lateral posterior margins; chaetotaxy reduced, prothoracic protergum with five, instead of seven setae, metatergum with the usual number; meso- and metathoracic proterga with only two setae, metaterga normal; all thoracic setae small and inconspicuous. Abdominal segments (fig. 2B) with paired sclerotized teeth at lateral margins of each tergal plate; plates well developed, slightly less than half width of segment; setae weakly developed, only true setae present, all very inconspicuous. Along posterior border of each tergal plate is a row of lightly sclerotized pegs, incomplete medially on metatergum; lateral posterior setae not differing greatly in length; inserted on tip of sclerotized lateral process; ventral mid-annular setae united by a sclerotized plate. Siphon (fig. 2D), with greatly elongated ventral processes; their bases expanded into quadrate plates; slightly more than twice as long as dorsal plate; hairy fringe of great length and remarkably even spacing of hairs; dorsal processes much curved, one-quarter length of ventral; dorsal plate with setae much reduced and no accessory setae; preanal plate oblong, setae weak and straight; adanal plates visible from dorsal surface and strongly toothed. Vestitural elements moderately sparse, well toothed; larger elements very conspicuous; present intersegmentally but not interannularly, except in more lateral region of each segment; no pronounced ambulatory elements.

Pupa.—Strongly flattened dorso-ventrally; ventral surface very weakly sclerotized, yellowish white in colour; dorsal surface strongly sclerotized. Respiratory horn (fig. 12) conical, folding into a depression on the side of the thorax; expanded apex with a circular depression surrounded by a ring of pits which join to felt chamber by 21–23 radially arranged tubes; felt chamber with delicate reticulate markings. Body segments with lateral margins fringed with teeth; terminal segment without dorsal teeth.

The larvae and pupae of *P. pulchra* occur in springs and clear flowing streams, where the former creep about on the undersides of stones and leaves, sufficiently close to the water to be kept wet by its lapping. The structural peculiarities which characterize this species, such as the dorso-ventral

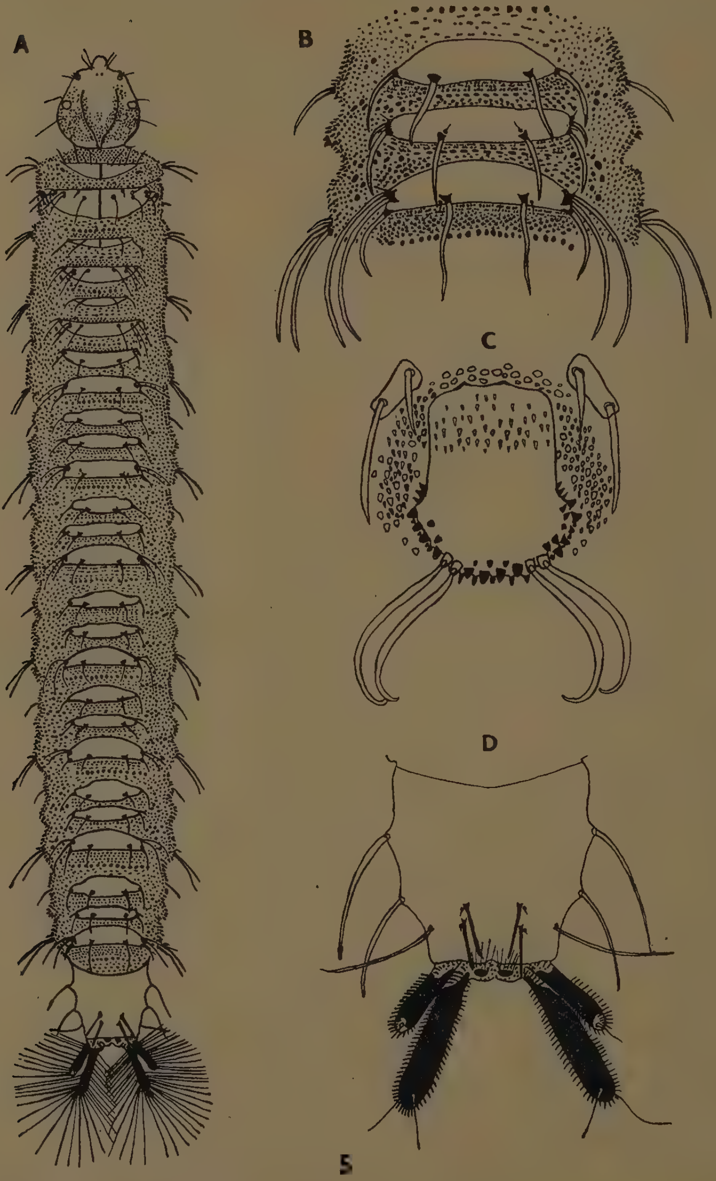

FIG. 5.—Larva of *P. diversa* Tonnoir. A, Whole larva, × 48; B, Fourth abdominal segment × 100; C, Preanal plate, × 153; D, Siphon, × 100.

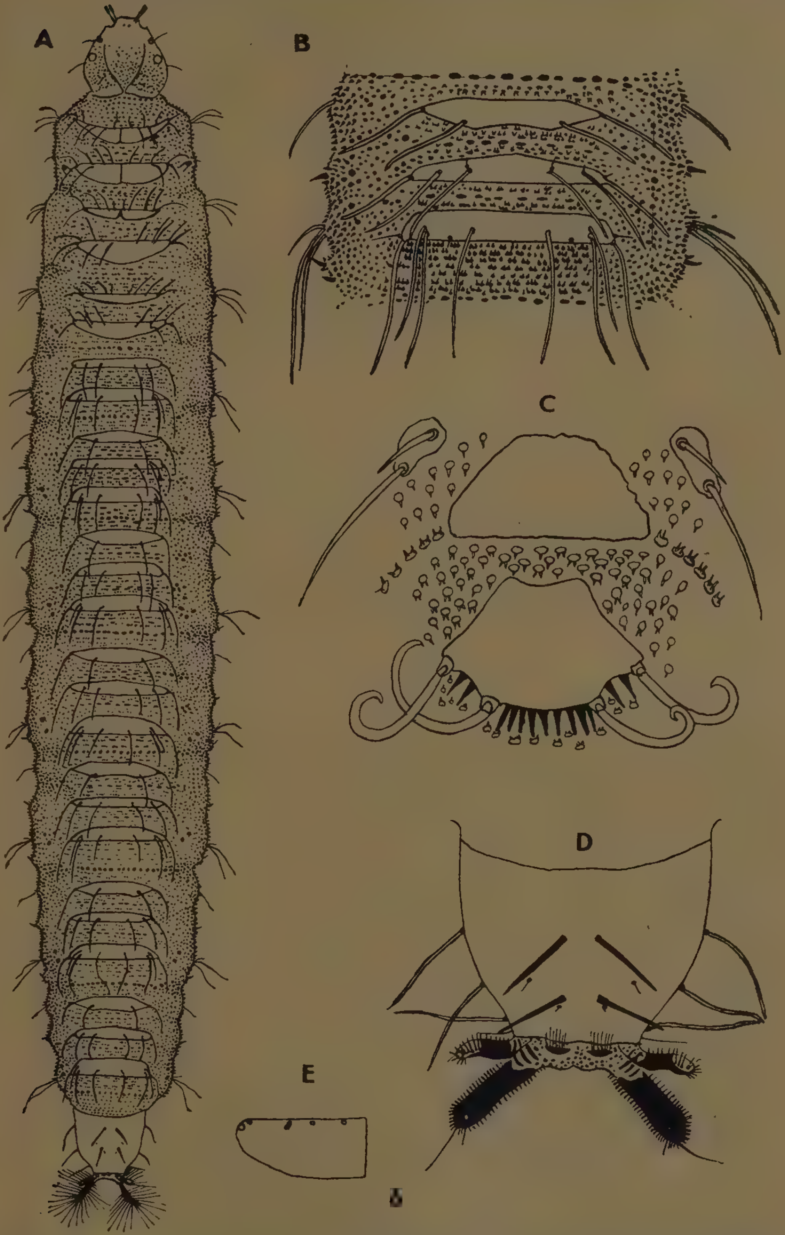

FIG. 6.—Larva of *P. exquisita* Eaton. A, Whole larva, × 34; B, Fourth abdominal segment, × 92; C, Preanal plate, × 190; D, Siphon, × 92; E, Prothoracic metatergum, × 76.

flattening, the lateral processes and the enlarged siphonal fringe, all serve to increase the area of contact between the larva and its substratum, and presumably assist in lessening the danger of being washed away. Features which characterize the species living in moss and algae, such as the well-developed dorsal setae and the curved preanal setae are here very reduced. The pupa fixes itself flush with the surface, and adheres solely by this means. As in the larva, there has been an increase in the area of contact by dorso-ventral flattening and the development of lateral spiny fringes, whilst the dorsal teeth of the terminal segment have been lost. Feuerborn (1923) states that he has found larvae of this species on stones and leaves in springs, and Eaton (1893) collected the adults by a small cliff stream in Somerset. The writer's material was collected from a small cool spring half-way up Thorpe Cloud, Derbyshire, and from a stream in Switherland Wood in Leicestershire. It was also abundant in Meanwood Beck, a small stream near Leeds.

P. trifasciata Meigen.

The larva of this species, and the related *P. calcilega*, can be distinguished from all others by the fact that they are thickly covered with a crust of lime, and occur only in springs and streams with a high lime content. The lime covering is formed round certain of the body setae which are greatly flattened and have the appearance of scythe blades ; they will be referred to as modified setae. When brought into the laboratory, specimens quickly lose their lime covering, as the water tends to become slightly acid, by putrefaction of the plant material, and the lime is dissolved.

Larva.—Fig. 3A. 5–6 mm. long, thickly covered with lime, greyish white in colour. Head markedly triangular, broadest just anterior to base ; ocelli more posterior than usual, denticles very numerous, carried forward to base of antenna (fig. 3E) ; mentum with 25–30 long, narrow, pointed teeth forming a hair-like fringe. Prothoracic protergum with setae 2–6 modified, 1 and 7 normal ; metatergum with conventional plan, all but the two small setae modified ; mesothoracic protergum with three small true setae and two modified accessory setae ; metatergum as in prothorax ; metathorax similar to mesothorax. Abdominal segments (fig. 3B) with well-developed tergal plates four-sevenths of segment width ; protergum with three modified accessory setae ; mesotergum with three modified accessory setae and three small plumose true setae ; metatergum with the usual four large setae modified, and the two small ones plumose ; setae well spaced, intersetal space one.quarter plate width ; lateral group on posterior annulus with the small seta modified, the two large ones normal ; anterior lateral seta modified ; ventral mid-annular seta broadened, on separate sclerotized plates ; post-annular setae with one short trichoid type, and one longer broad seta, hooked at tip. Siphon (fig. 3D) with ventral processes four-tenths length of dorsal plate ; dorsal processes one-third length of ventral ; anterior two, of the four main lateral setae, are modified ; three modified accessory setae dorsally, with bases one behind the other ; anterior one larger ; preanal plate with setae strongly curved and set close together ; sclerotized tubercles on posterior margin. Vestitural elements lightly sclerotized ; larger elements not present interannularly ; lateral elements with hairy fringes, particularly on each abdominal middle annulus ; ambulatory elements simple points, best developed on each anterior annulus.

Pupa.—Not covered with lime ; respiratory horn (fig. 15) four to five times as long as broad, cylindrical and untapered, when seen in posterior view ; outer surface with faint, scale-like markings ; pits in a simple double row in apical portion of horn, 14–16 in each row ; felt chamber with a constriction immediately prior to where it begins to

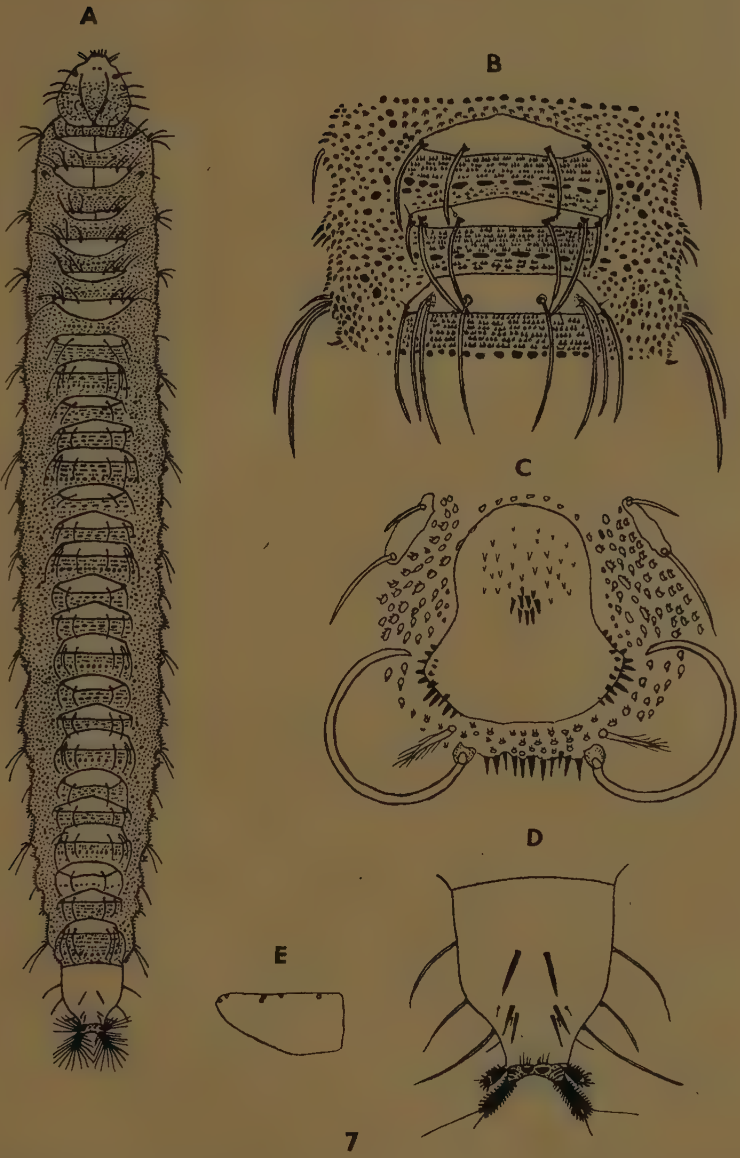

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FIG. 7.—Larva of *P. fallax* Eaton. A, Whole larva, × 34 ; B, Fourth abdominal segment, × 92 ; C; Preanal plate, × 190 ; D, Siphon, × 92 ; E, Prothoracic metatergum, × 76.

expand to meet the pit-bearing area. Posterior fringe of dorsal surface of seventh abdominal segment (fig. 26), with two or three points between medial sensillae; sensilla element awl-like; more lateral paired sensillae with one trichoid and one awl-like element. Dorsal teeth of terminal segment appearing bifid; consisting of a cuticular point with an awl-like sensilla half-way up.

The modified, lime-bearing setae of this species are so characteristic that the only species with which it might be confused is *P. calcilega*, which also bears them. From the figure Feuerborn (1923) gives of the posterior two segments of this larva, it would appear to be differentiated from *P. trifasciata* by the greater number of modified accessory setae on the tergal plates. The protergum bears a large one at the corner and three smaller ones more medially, whilst the mesotergum has a large corner one and five smaller ones medially. In addition, there is an extra small modified seta on the dorsal plate of the siphon, making three small and one large modified seta in each half.

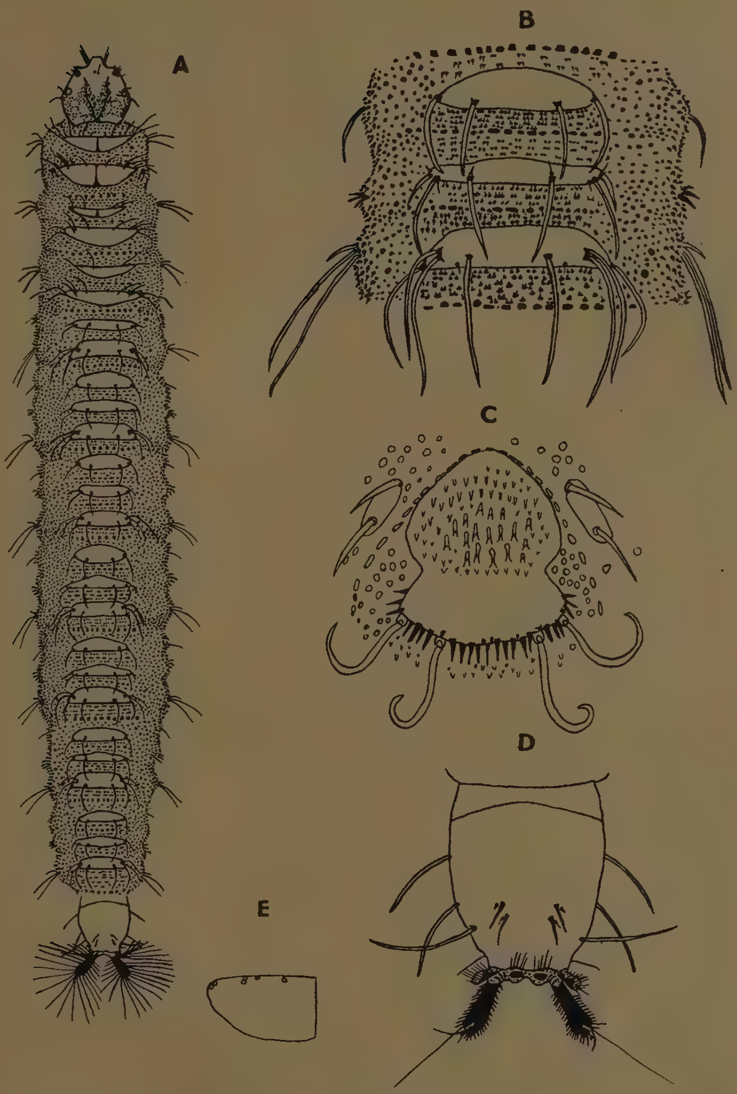
One of the British species of the related genus *Telmatoscopus*, *T. decipiens*, has a larva which lives in limy springs, and is covered with a thick lime crust. It can be distinguished from the two species of *Pericoma* just described, by the shape of the head, which is oval. The markedly triangular head is limited to the three species, *P. pulchra*, *P. trifasciata* and *P. calcilega*.

Feuerborn (1923) records *P. trifasciata* and *P. calcilega* from limy springs and streams. The material of *P. trifasciata* described in this paper was collected from the small springs and streams that flow from the steep rock faces lining the roads in North Derbyshire. These streams are rich in calcium carbonate, and a limy crust covers the rock face and even the leaves of the moss that grows there. Amongst the moss of some springs and streams in Millers Dale these larvae were found in great abundance.

Feuerborn (1923) suggests that the thick lime covering is an adaptation to reduce desiccation, thereby enabling the larva to penetrate further from the stream margin, than would otherwise be possible. In favour of this suggestion it can be said firstly, that the body setae are unlike those of non-limy species and the lime does adhere to them, though precisely why they assume the form they do is not clear. Secondly, it is only the setae of the dorsal and lateral surfaces which are so modified. The ventral setae are quite normal, and there is no lime covering on the ventral surface. It may be assumed that evaporation from the ventral surface, in contact with the damp ground, is less than from the dorsal, and there is, therefore, less need for a lime covering there. Thirdly, against the view that the lime covering is fortuitous, and merely the result of precipitation from a saturated solution, is the fact that larvae of other species of *Pericoma*, notably *P. fuliginosa* and *P. exquisita*, were found, along with *P. trifasciata* in the Millers Dale streams, and were quite free from any lime covering. It is, however, so easy to free larvae of this species from the chalky investment, that it should not be difficult to put Feuerborn's hypothesis to experimental verification.

P. neglecta Eaton.

The larva of this species was the first *Pericoma* larva to be described in any detail. Miall (1895) described it under the name of *P. canescens*, a closely-related species, distinguished in the adult only by differences in the male genitalia. Miall's paper was read in title before the Entomological



8

Fig. 8.—Larva of *P. blandula* Eaton. A, Whole larva, × 34 ; B, Fourth abdominal segment, × 92 ; C, Preanal plate, × 190 ; D, Siphon, × 92 ; E, Prothoracic metatergum, × 76.

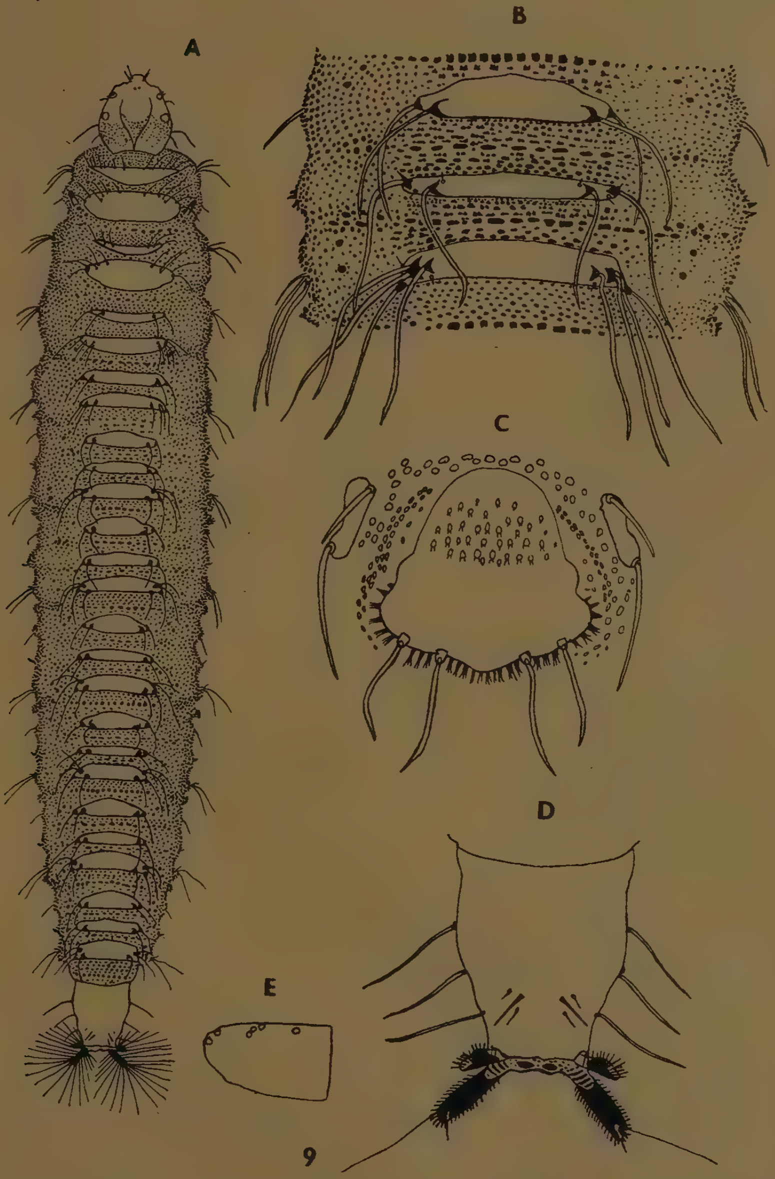
Society of London on 6th February, 1895, and Eaton published his description of *P. neglecta* in May, 1893. It is impossible to ascertain how long Miall's paper was in the press, and how long, before submitting it, he had his material identified, but there is a strong probability that his mistake was inevitable, resulting from the fact that no distinction had been drawn between the two species at the time. Grünberg (1910) copied his error, as also did Feuerborn (1913). By 1923, however, Feuerborn had bred out the larvae of both species, and in his paper pointed out the great difference that exists between them. Since Feuerborn's 1923 account is very incomplete, there is still a need for a thorough description of *P. canescens*.

Larva.—Fig. 4A. 6–8 mm. long, normally free from detritus, black. Head oval, broadest just behind middle; denticles not reaching beyond line joining anterior margin of ocelli; mentum bearing a row of 18–20 short, bluntly-pointed teeth. Prothoracic chaetotaxy on conventional plan; mesothoracic protergum with seta 1 moderately long and fringed, 2 and 3 not fringed; metathoracic protergum with one long accessory seta, one short true seta near its base, and two long true setae; metaterga with two setae medially. Abdominal segments (fig. 4B), with tergal plates equal to half segment width; two protergal setae, chaetotaxy otherwise on conventional plan; setae subequal, reaching just beyond middle of next annulus; grouped close to plate margin, so that intersetal space is two-thirds of plate width; all setae mounted on prominent sclerotized bosses; tergal plates largely free from vestitural elements, except for a few circular denticles in centre of each plate, more numerous on metatergum than protergum. Ventral mid-annular setae united by sclerotized plates; post-annular setae not hooked at tip. Siphon (fig. 4C and D) with processes long; ventral processes four-fifths of dorsal plate, dorsal processes four-fifths length of ventral; hairy fringes very long; margin of siphon indented between bases of main lateral setae; a single accessory seta present dorsally; separated from its partner by a distance slightly less than half siphon width at same level; preanal plate with setae spaced equidistantly, not obviously curved; space between filled with comb-like elements with hairy fringes. Vestitural elements moderately toothed, more so at lateral margins; each abdominal annulus with a row of ambulatory elements mid-ventrally, consisting of comb-like scales with hairy fringes.

Pupa.—Respiratory horn cylindrical in posterior view, broader apically in side view (fig. 16), five times as long as broad; covered, except in pitted region, with scale-like markings; pits arranged in a simple double row, 12–14 in one row, 18–20 in other; confined to upper third of horn. Fringe on posterior margin of dorsal surface of seventh abdominal segment (fig. 22) with two or three pointed teeth between medial sensillae; these consist of an awl-like blade mounted on a prominent sclerotized boss; more lateral paired sensillae with one trichoid, one awl-like element. Dorsal teeth of terminal segment formed from awl-like sensillae at tips of outwardly-curving processes.

The larva of this species is most likely to be confused with that of *P. diversa* which has a similar siphon and often occurs along with it. It is readily distinguished from *P. diversa* by the common plates linking the ventral mid-annular setae, and the absence of hooked post-annular setae.

The larva of *P. neglecta* is found on mill weirs and waterfalls in clumps of moss which, though continually drenched by the falling water, are not completely submerged. By means of its strongly developed dorsal setae, and its habit of curling around moss stems, it maintains a firm hold on its surroundings in spite of the buffets of the cascade. The material described in this paper was collected on a small waterfall on Meanwood Beck, near Leeds, on the falls of the River Dove, Derbyshire, and the weirs of Bradgate stream, Bradgate Park, Leicestershire.



9

Fig. 9.—Larva of *P. pseudexquisita* Tonnoir. A, Whole larva, × 34; B, Fourth abdominal segment, × 92; C, Preanal plate, × 190; D, Siphon, × 92; E, Prothoracic metatergum × 76.

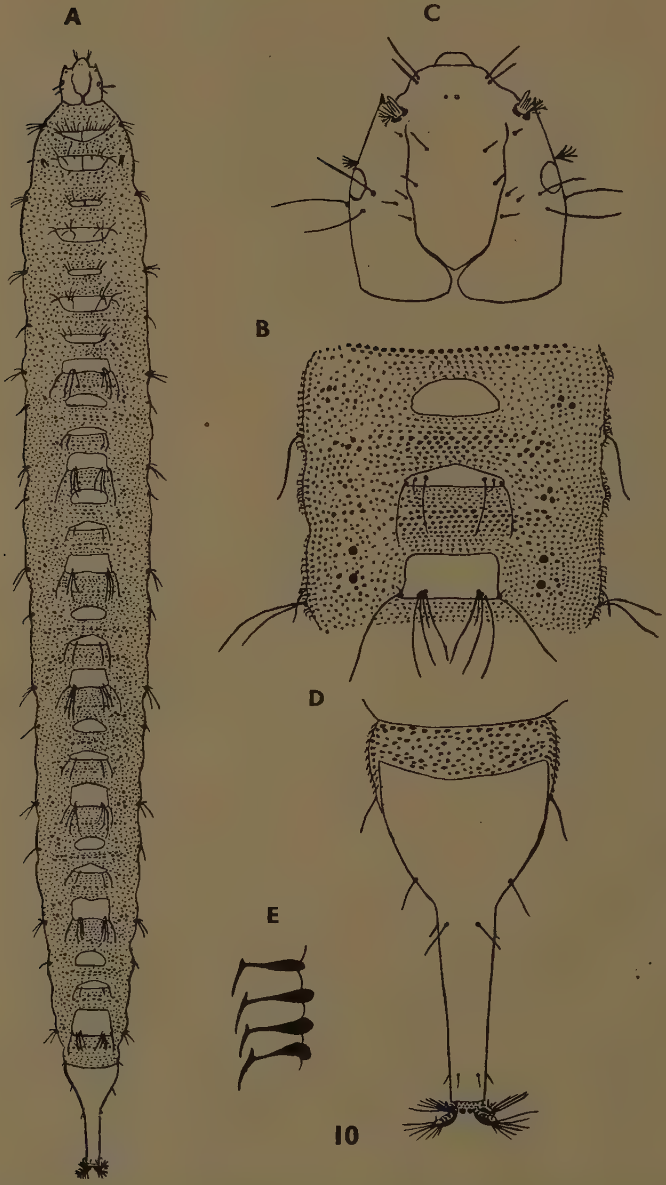


FIG. 10.—Larva of *P. fusca* Macquart. A, Whole larva, × 20 ; B, Fourth abdominal segment, × 53 ; C, Head, × 92 ; D, Siphon, × 53 ; E, Vestitural elements of abdomen, seen in profile, × 427.

P. canescens Meigen.

No material of this species has been collected by the writer, but according to Feuerborn's (1923) figure of the posterior three segments of the larva, it can at once be distinguished from *P. neglecta* by the numerous accessory setae on the lateral margins of the siphon, and the shorter siphonal arms. The tergal plates look very like those of *P. neglecta*, with strongly developed setae, set on sclerotized bosses and located at the margins of the tergal plates. The group of circular denticles in the centre of each plate is another point of similarity. The more lateral location of the tergal setae is a feature serving to distinguish it from the larva of *P. trivialis*.

P. canescens occurs in very different habitats from *P. neglecta*. Feuerborn (1923) records it from rotting leaves on stream margins, and Mayer (1938) includes it in his survey of the fauna of beech tree holes.

P. diversa Tonnoir.

Larva.—Fig. 5A. 5–6 mm. long, normally free from detritus. Head oval, broadest just behind middle ; denticles rather feeble but reaching around ocellus to antenna base, absent from anterior central region ; mentum with a closely set row of 25–30 long, fine, pointed teeth having the appearance of a fringe of hairs. All setae very thick and short ; prothoracic chaetotaxy on conventional plan ; mesothoracic protergum with two large accessory setae and three small true ones ; metatergum on conventional plan ; metathoracic terga as in mesothorax. Abdominal segments (fig. 5B), with tergal plates half segment width ; two protergal setae ; three mesotergal setae ; mesotergal 3 is a short, stumpy seta, one-quarter length of mesotergal 2 ; metatergal setae on conventional plan ; setae well spaced, intersetal space one-third plate width ; setae reaching only to middle of next tergum ; ventral mid-annular setae with separate sclerotized plates around their bases ; post-annular setae with one strongly hooked at tip. Siphon (fig. 5D), with ventral processes nine-tenths length of dorsal plate ; dorsal processes six-tenths length of ventral ; hairy fringes long ; margins of siphon indented between bases of main lateral setae, which are short and thick ; two accessory setae dorsally, with their bases close together, separated from partners of opposite side by a distance one-quarter of siphon width at same level ; preanal plate (fig. 5C), with posterior setae very strongly curved ; the two of each side with their bases close together ; remainder of posterior margin covered with strong, black, heavily sclerotized tubercles. Vestitural elements moderately toothed ; a group of strong, pointed teeth on the lateral margin of each middle annulus of abdominal segments ; ambulatory elements comb-shaped, ventrally, on each abdominal annulus.

Pupa.—Respiratory horn (fig. 14) five times as long as broad, dilated apically ; double pit row commences on posterior face one-third way down, and after 13–15 pairs of pits, divides into two ; longer portion curves over apex and just commences descending anterior face before terminating ; 11–12 pits in length ; shorter portion runs off to one side before terminating ; 8–10 pits in length ; division of pit row may be difficult to see as it occurs at apex. Posterior fringe of dorsal surface of seventh abdominal segment (fig. 25) with one or two points between medial sensillae ; sensilla element in form of a long, curved, awl-like blade ; mounted on long sclerotized bosses ; more lateral paired sensillae with one awl-like and one trichoid element. Dorsal tooth of terminal segment formed from short awl-like sensilla with cuticular point at one side.

This species is less common than the others, and the larva has not been taken sufficiently frequently to enable much information about its habitat to be given. It has only been found in the moss tufts kept wet by the spray from the waterfalls in Bradgate Park, Leicestershire. This habitat it shares with *P. neglecta*, but does not appear to venture so far into the really turbulent region as does the latter species.

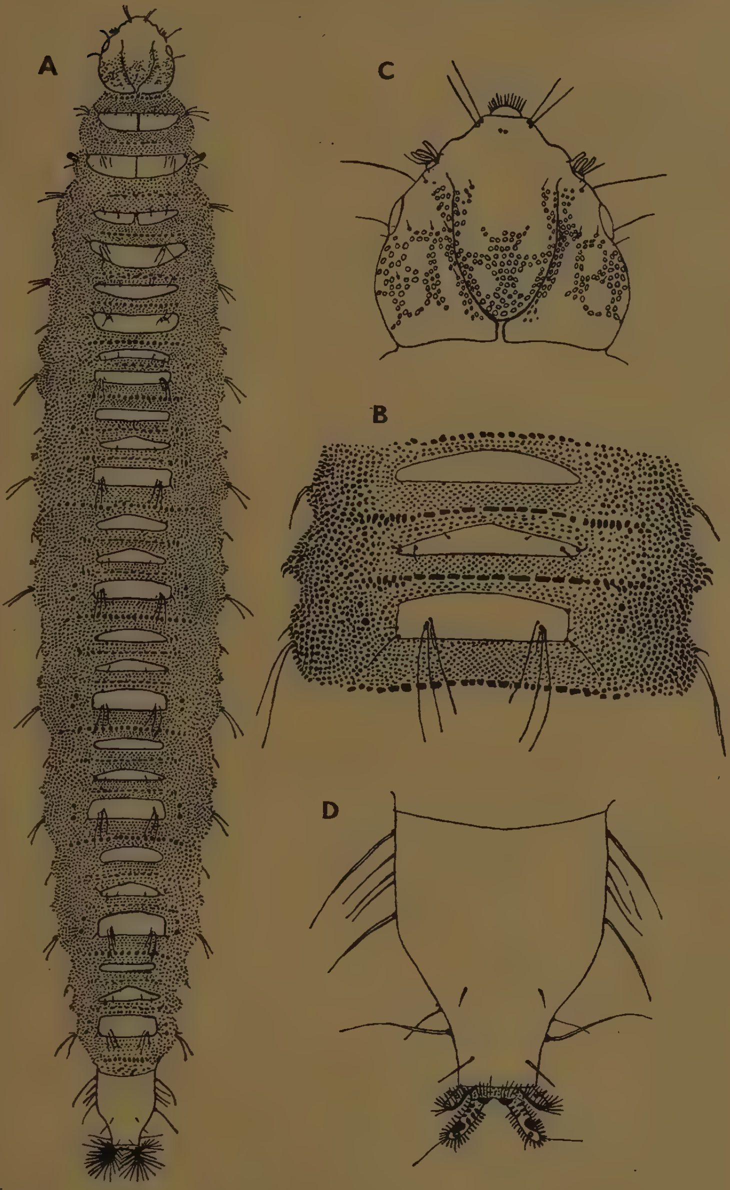
The four species *P. exquisita*, *P. fallax*, *P. blandula* and *P. pseudexquisita* have larvae with, superficially, a very similar appearance. Moreover, they are all to be found in mats of the alga *Cladophora*, and two, or even three, of these species may occur together. Providing that the siphon has been sufficiently cleared for the dorsal accessory setae and the preanal plate to be seen, however, they can be readily distinguished from one another.

P. exquisita Eaton.

Feuerborn (1927) figures the anterior four segments of what he claims to be the larva of *P. exquisita*. It is almost impossible to judge from the anterior segments alone, what species he was dealing with, but it is unlikely to have been *P. exquisita*, because this species is absent from the Continent (Tonnoir, 1940), and, moreover, the figure of the pupal horn on the opposite page, also claiming to be that of *P. exquisita*, is clearly that of some other species.

Larva.—Fig. 6A. 5–6 mm. long, usually free from detritus, black. Head oval, broadest just behind middle ; denticles present to anterior margin of ocelli ; mentum with a large tooth at both ends, connected by an undulating border with a fringe of 25–30 long, narrow, pointed teeth anterior to it. All setae long and well developed ; prothoracic protergum with all seven setae long ; metatergum (fig. 6E) with seta 2 separated from (3 + 4) by a distance greater than the width of a seta base ; meso- and metathoracic proterga with one short true seta, two long true setae, and two long accessory setae ; metaterga on conventional plan. Abdominal segments (fig. 6B) with tergal plates one-half body width ; two protergal setae, chaetotaxy otherwise on conventional plan ; inter-setal space one-third plate width ; setae long, subequal, reaching beyond middle of next tergal plate ; ventral mid-annular setae with separate sclerotized plates ; post-annular setae with one hooked at tip. Siphon (fig. 6D), with ventral processes slightly more than half length of dorsal plate ; dorsal processes slightly more than half ventral ; no accessory setae laterally ; two present dorsally ; anterior one separated from its partner of opposite side by a distance one-eighth of siphon width at same level, and from the more posterior one of the same side by twice this distance ; preanal plate (fig. 6C) unique in being divided transversely into two ; posterior half with usual two curved setae on posterior margin ; of equal length and equally spaced ; posterior fringe of about 12 long, pointed teeth. Vestiture showing large elements present interannularly as well as intersegmentally ; prominent teeth present laterally on the middle annulus and posterior to the lateral posterior setal group, of each abdominal segment ; ambulatory elements simple, pointed teeth best developed on each anterior annulus.

Pupa.—Respiratory horn three times as long as broad ; felt chamber divided into three, one branch lying alongside main stalk in posterior third, one running across in middle third, and one curving round the apex and partly down one side (fig. 17). Other smaller branches may arise in various positions. Double pit row following course of branches of felt chamber ; each primary pit communicating on outer side with one secondary pit, so horn is covered with pairs of pits ; virtually the whole of dorsal surface is covered with these bands of double pits ; between 80 and 100 pairs of primary pits in all. Posterior fringe of dorsal surface of seventh abdominal segment with none to two points between medial sensillae which have sickle-shaped elements ; dorsal teeth of terminal segment formed from sensillae of same type.



11

FIG. 11.—Larva of *P.* (*Ulomyia*) *fuliginosa*. A, Whole larva, × 30; B, Fourth abdominal segment, × 76; C, Head, × 92; D, Siphon, × 92.

P. fallax Eaton.

Larva.—Fig. 7A. 5–6 mm. long; normally free from detritus; black. Head oval, broadest just behind middle; denticles carried forward to the level of anterior margin of ocelli; mentum with a fringe of 18–24 narrow, pointed, hair-like teeth. Setae only of moderate length; thoracic chaetotaxy on conventional plan, except that meso- and metathoracic proterga have all three true setae large, and two small accessory setae in addition; prothoracic metatergum (fig. 7E) with seta 2 separated from (3 + 4) by a distance greater than width of seta base. Abdominal segments (fig. 7B), with tergal plates seven-tenths of segment width; protergum with two accessory setae, mesotergum with three accessory setae; mesotergal 3 is a short stumpy hair, only one-third length of mesotergal 2; metatergum with setae on conventional plan; apart from mesotergal 3, setae subequal, reaching beyond next tergum; well spaced, intersetal space one-third plate width; ventral mid-annular setae on separate sclerotized plates, post-annular setae with one hooked at tip. Siphon (fig. 7D) with ventral processes one-quarter length of dorsal plate; dorsal processes six-tenths length of ventral; three accessory setae dorsally; longer anterior one, separated from its partner of opposite side, by a distance one-fifth to one-sixth of siphon width at same level, and from the more posterior two setae of the same side by twice this distance; preanal plate (fig. 7C), unique in that posterior setae are not on its border but behind it; inner seta is greatly elongate and curved in a semicircle; outer one is short, uncurved and fringed; between them lies a row of sclerotized points. Vestitural elements moderately toothed; larger elements present interannularly as well as intersegmentally; prominent teeth present laterally on the middle annulus, and posterior to the lateral posterior setal group, of each abdominal segment; ambulatory elements simple points best developed on each anterior abdominal annulus.

Pupa.—Respiratory horn (fig. 20), two and a half times as long as broad; felt chamber dividing into two in middle of horn, one branch running backwards parallel with main stem for a short distance, the other ascending to the apex and curving backwards for a short distance; pit row dividing and following branches of felt chamber; from each primary pit a ribbon of from 3–6 secondary pits curves round the horn; 55–60 primary pits in each row. Posterior abdominal fringes and terminal teeth as in *P. exquisita.*

P. blandula Eaton.

Larva.—Fig. 8A. 4–5 mm. long, free from detritus, black. Head oval, broadest just behind middle; denticles rather sparse, reaching forward to level of anterior margin of ocellus; mentum with a fringe of 16–20 narrow, pointed, hair-like teeth. Setae moderately developed; thoracic chaetotaxy on conventional plan except that meso- and metathoracic proterga have one long and one short accessory setae in addition to the three small true setae; prothoracic metatergal 2 separated from (3 + 4) by a distance greater than the width of a seta base (fig. 8E). Abdominal segments (fig. 8B) with tergal plates one-half segment width; two protergal setae, three mesotergal setae; mesotergal 3 is a short, stumpy seta, one-half to one-third length of mesotergal 2; metatergum with setae on conventional plan; setae, apart from mesotergal 3, subequal, reaching to middle of next annulus; well spaced, intersetal space slightly less than half plate width; ventral mid-annular setae with separate sclerotized plates; post-annular setae with one hooked at tip. Siphon (fig. 8D) with ventral processes one-third length of dorsal plate; dorsal processes four-tenths length of ventral; two accessory setae present dorsally; more anterior, separated from its partner of opposite side, by a distance between one-third and one-half siphon width at this level, and from more posterior seta of same side by one-third this distance; preanal plate with posterior setae subequal, strongly curved; posterior fringe of lightly sclerotized, pointed teeth. Vestitural elements moderately toothed; larger elements interannularly as well as intersegmentally; prominent teeth present laterally on the middle annulus of each abdominal segment ; ambulatory elements simple pointed teeth on each abdominal annulus.

Pupa.—Respiratory horn (fig. 18) twice as long as broad ; felt chamber three-branched, with a branch both sides of the main stem and one curling over the apex ; pit row following branches of felt chamber ; from each primary pit one secondary pit is given off, so a paired structure is produced ; 55–60 primary pits in each row. Posterior fringe of dorsal surface of seventh abdominal segment, and terminal teeth, as in *P. exquisita.*

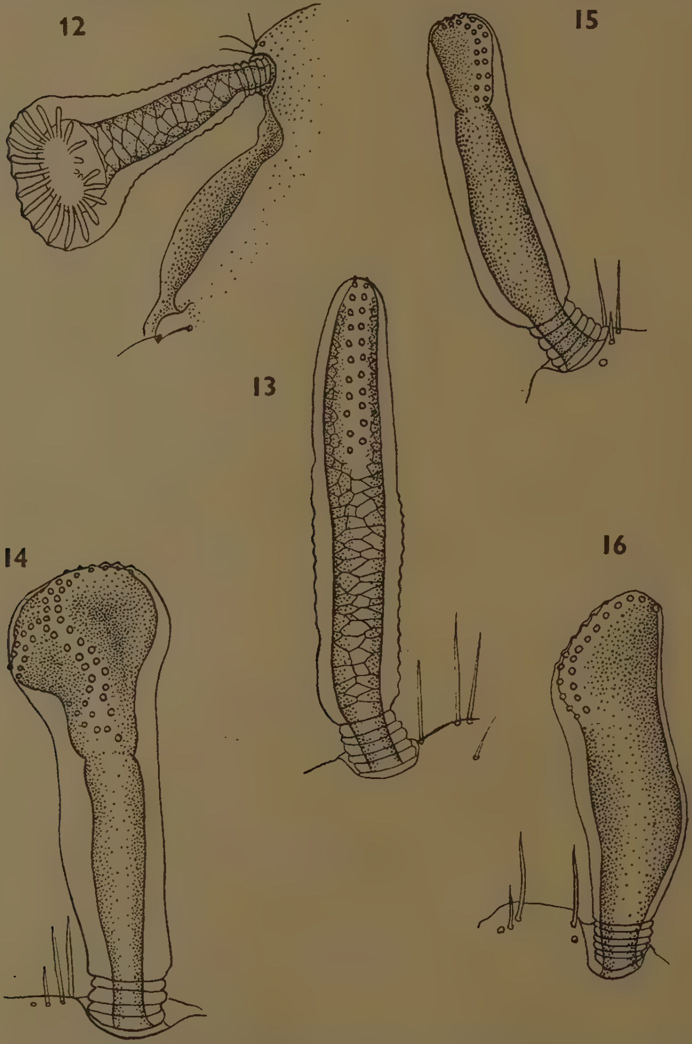
P. pseudexquisita Tonnoir.

Larva.—Fig. 9A. 5–6 mm. long, free from detritus, black. Head oval, broadest just behind middle ; denticles not reaching beyond posterior margin of ocelli ; mentum with a fringe of 20–25 narrow, pointed, hair-like teeth. Setae long and well developed ; prothoracic protergum with all seven setae long, there being little difference in size ; mesothoracic protergum with three large accessory setae, and three small true setae ; metathoracic protergum with two large accessory setae and three small true ones ; prothoracic metaterga with seta 2 separated from (3 + 4) by a distance equal to, or less than, the width of a seta base (fig. 9E). Abdominal segments (fig. 9B), rather wider than in previous three species ; tergal plates slightly more than half segment width ; two protergal setae ; only two mesotergal setae, instead of the usual three, mesotergal 3 of the other species here being absent ; metatergal setae on conventional plan ; setae reaching beyond middle of next plate ; crowded to lateral margins, so intersetal space is from half to seven-tenths of plate width ; ventral mid-annular setae with separate sclerotized plates around their bases ; post-annular setae not hooked. Siphon (fig. 9D), with ventral processes four-tenths length of dorsal plate ; dorsal processes four-tenths length of ventral ; a single accessory seta dorsally, separated from its partner of opposite side by a distance one-half siphon width at same level ; the two small true setae usually present in this position are larger than in the previous three species ; preanal plate with posterior setae weak, and not obviously curved ; posterior fringe of comb-like elements. Vestitural elements rather more heavily sclerotized than in the three previous species ; larger elements present interannularly as well as intersegmentally ; tooth-like elements on lateral margin of each middle annulus not strongly developed ; ambulatory elements in form of peg-like structures arranged in a transverse row on each abdominal annulus.

Pupa.—Respiratory horn (fig. 19), three times as long as broad ; felt chamber usually undivided but bent back on itself apically ; sometimes a short branch to the felt chamber is given off half-way up ; pit row following felt chamber, between 37 and 40 pits in each row ; from each primary pit a ribbon of up to seven secondary pits runs off and partly encircles horn. Fringes of abdominal segments and teeth of terminal segment very similar to those of *P. exquisita.*

The four species of larvae just described all occurred in the mats of algae, chiefly *Cladophora*, which clothed stones projecting from the stream in Bradgate Park, Leicestershire. *P. exquisita* and *P. pseudexquisita* were the most commonly occurring species, *P. blandula* less common, and *P. fallax* rather scarce. Larvae of the first two species were taken at other localities ; *P. exquisita* was often present in the spray-drenched moss from the River Dove waterfalls, and the streams in Millers Dale, in Derbyshire. *P. pseudexquisita* was collected from *Cladophora* mats clinging to lock gates both on the Wollaton Canal, Nottinghamshire, and the River Ouse, in Huntingdonshire. They were, however, so often present, and in such abundance, in the algal mats at Bradgate, that these must rank first in importance in their list of habitats.

Not only are the larvae of these four species superficially rather alike, but their pupae differ from the others in the increased size and number of their pits. The addition of an extra pit, in *P. exquisita* and *P. blandula*, and a ribbon of pits in *P. fallax* and *P. pseudexquisita*, to the lateral margin of each primary pit, is a feature that occurs in no other *Pericoma* pupa so far described. It has the effect of greatly increasing the area of pit membrane through which gaseous exchange may occur. By measuring the area of ten



Figs. 12–16.—Respiratory horns of *Pericoma* pupae, all × 293. (12) *P. pulchra*, (13) *P. fusca*, (14) *P. diversa*, (15) *P. calcilega*, (16) *P. neglecta*.

pits at random, averaging the result and multiplying by the total number of pits, it has been possible to make an estimate of just how much greater is the area. The actual number of pits varies from one individual to another, and the figures given refer to the result obtained from a single specimen in each case, as only in preparations in which the horn is exceptionally well displayed, is it possible to count the pits at all accurately. Taking *P. neglecta* as a standard, the surface of the pit membrane is thirty-four times as great in *P. blandula*, fifty-seven in *P. fallax*, sixty-two in *P. pseudexquisita* and ninety in *P. exquisita*. These differences are the more remarkable when it is realized that all the four species concerned are small, and have pupae considerably smaller in bulk than *P. neglecta*. Why these enormously greater respiratory surfaces should be needed by pupae living in algal mats, compared with ones living in moss or leaf mould is not clear. So little is known about the physical processes involved in the functioning of the dipterous pupal respiratory horn that it is pointless to speculate further.

P. fusca Macquart.

The last two body segments of the larva of this species were figured by Feuerborn (1923), and are sufficient to indicate that it differs considerably from that of the other species so far described. It bears a strong superficial resemblance to a *Psychoda* larva, for the vestiture is rather sparse, giving the larva a whitish appearance, and the siphon is greatly elongated, as is often the case in larvae of that genus (Satchell, 1947). The presence of a preanal plate, and the character of the antenna, are alone sufficient, however, to indicate that it is not a *Psychoda* larva.

Larva.—Fig. 10A. 9–10 mm. long, very slender and vermiform, free from detritus covering; whitish. Head markedly quadrate (fig. 10C), broadest at the middle; surface smooth owing to absence of denticles; mentum not toothed. Setae thin and pale; thoracic chaetotaxy on conventional plan except that the most medial four setae of each metaterga are grouped together. Abdominal segments (fig. 10B) with tergal plates, only twice as wide as long, one-quarter width of segment; no protergal setae; mesotergal 1 long, 2 short, 3 long; these are the three true setae normally present; no accessory mesotergal setae; metatergal 1 and (2 + 3) in a compact group near the lateral margin; intersetal space one-half plate width; setae long and slender, reaching to next tergal plate; ventral mid-annular setae with their bases united by a sclerotized plate; post-annular setae not hooked. Siphon (fig. 10D), exceptionally long and slender, with a gently tapering terminal portion twice as long as the swollen basal region; processes reduced, ventral process between one twenty-fifth and one-thirtieth length of siphon; no accessory setae; preanal plate with setae weak and not curved. Vestitural elements sparsely placed; larger elements interannularly as well as intersegmentally; spines of vestitural elements project vertically out from base, and are then bent through ninety degrees (fig. 10E). No ambulatory elements present.

Pupa.—Respiratory horn (fig. 13), slender, five to six times as long as broad. Pits in a simple double row, extending four-tenths of distance down horn, 15–16 in each row; felt chamber with a fine reticulate meshwork on its surface. Posterior dorsal fringe of seventh abdominal segment with ten or so short, blunt teeth between medial sensillae, which are trichoid (fig. 24). Dorsal surface of terminal segment not bearing the usual paired teeth, but instead a single, median, bifid, strongly rugose, spade-like process.

Feuerborn (1923) mentions that the larva of *P. auriculata* Walker is similar to that of *P. fusca*, and since these two species are another example of geminate species, or species pairs, the possibility exists that their larvae are indistinguishable as is the case with *P. trivialis–P. nubila*. Until, however, the larva of *P. auriculata* has been described, it cannot be ascertained just how alike they are.

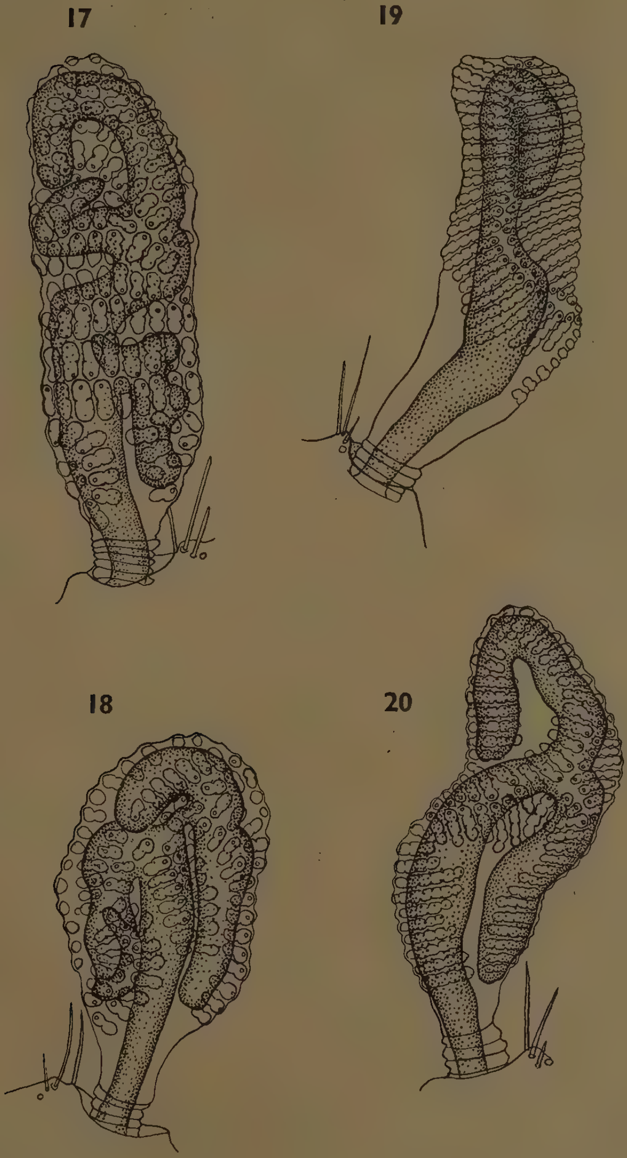
The material described in this paper was collected in soft leaf mould bordering a stream in Switherland Wood, Leicestershire. This stream runs through an area of marshy ground overhung by alders, and their leaves had rotted down to a moist compost in which no trace of their structure could be seen. In this material the larvae occurred. Feuerborn (1923) mentions that this larva lives in soft, rich leaf mould, and that it does not crawl about on the surface, but burrows right into it. Eaton (1893) states that the adults abounded in a wood containing a pond in Somerset, and Macquart (1824) who described the species, mentions that he collected it in a wood.

In its habit of burrowing into leaf mould, this larva has adopted a mode of life differing from that of the majority of species of *Pericoma*, a difference that is reflected in its structure. The elongation of the siphon, and of the body itself, enables it to explore a greater depth of material whilst still retaining a communication with the atmosphere. The reduction of the dorsal setae, and the loss of all accessory setae is to be expected; such structures would impede a burrowing larva. Similar modifications have occurred in larvae of the genus *Psychoda* (Satchell, 1947) the majority of which live in cattle dung, where somewhat similar conditions prevail (Satchell, 1948*a*). It is of interest that a similar type of *Pericoma* larva occurs in America, for Johannsen (1934) has described an unidentified species of *Pericoma* larva, which he designates Species A, in which the siphon is similarly elongated. It is not the larva of *P. fusca*, as the chaetotaxy differs, but it shows a number of features in common with it.

P. (*Ulomyia*) *fuliginosa* Meigen.

Walker (1856) has described the larva of what he claims to be this species, then known as *Ulomyia hirta* L., and says that it "has, like a dorsibranchial Annelid or *Phyllodoce*, down the back, two rows of acute, lanceolate, foliaceous, branchia-like appendages; each row consists of three pairs on each segment." This sentence calls to mind a larva so different from the one about to be described, that it must be concluded that he was dealing with some other species.

Larva.—Fig. 11A. 6–7 mm. long, normally free from detritus; intensely black. Head (fig. 11C) oval, broadest just behind middle, denticles rather sparse in centre, but extending along suture beyond level of ocellus; mentum with 12–14 short, bluntly-pointed teeth. Chaetotaxy of whole larva obscured by weak development of setae, and extension of vestitural elements over tergal plates. Prothoracic protergum with reduced setae on conventional plan, metatergum with a group of four setae half way between mid-line and margin and two more at margin; meso- and metathoracic proterga with three minute true setae, metaterga as in prothorax. Abdominal segments (fig. 11B) with plates rather less than half of body width; no protergal setae; three minute mesotergal setae; metatergum with 1 and (2 + 3) forming a group close to the lateral margin; intersetal space two-thirds of plate width; setae thin and colourless but of moderate length, extending to next annulus; ventral mid-annular setae with separate sclerotized plates, the outer one larger; post-annular setae unhooked. Siphon (fig. 11D) with very short processes,



FIGS. 17–20.—Respiratory horns of *Pericoma* pupae, all × 293. (17) *P. exquisita*, (18) *P. blandula*, (19) *P. pseudexquisita*, (20) *P. fallax*.

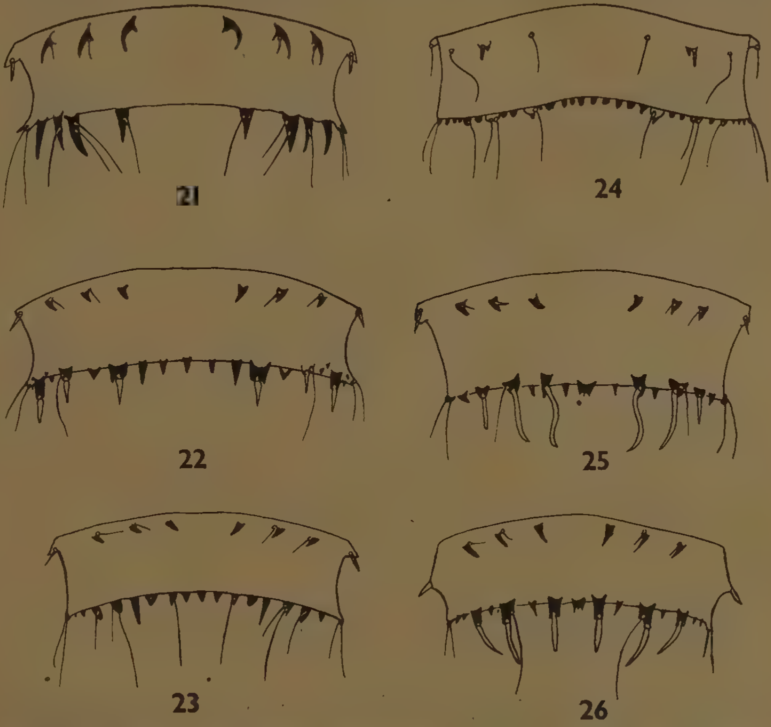
ventral pair angulated as in *P. trivialis*, not more than one-ninth length of dorsal plate; dorsal processes one-half length of ventral; main lateral setae inconspicuous, no accessory setae; preanal plate almost quadrate, setae weak and uncurved. Vestitural elements largely devoid of spines; mid-dorsally, between tergal plates, regularly arranged in close rows, like nail-heads; enlarged elements occurring interannularly as well as intersegmentally; short, blunt teeth present laterally; ambulatory elements in form of short, blunt pegs, best developed on each anterior annulus of abdominal segments.

Pupa.—Respiratory horn similar to that of *P. neglecta* (fig. 16), though possibly slightly longer and with 2–3 more pits in each row. Posterior fringe of dorsal surface of seventh abdominal segment with medial sensillae widely spaced (fig. 21), and no teeth or points between; sensillae consisting of trichoid elements inserted on long, pointed, sclerotized teeth. Terminal segment with dorsal teeth, weak cuticular points; a short spiny sensilla mounted half-way up.

The larva of *P. fuliginosa* occurs in decaying vegetation on the margins of streams, and has been collected from all the localities that have been visited regularly. In contrast to *P. trivialis*, however, it tends to be confined to cracks and crevices, to crawl on the underside of sticks and detached bark, and to work its way through the layers of decayed vegetation, rather than crawl about on the surface. The two species often occur together however. The loss of the accessory setae has occurred in this species, as it has in *P. fusca*, but in other respects it is not so greatly modified for living within, rather than on, its substrate.

With the completion of these larval descriptions it only remains to consider how many of the criteria previously used by authors for separating *Pericoma* larvae from those of related Psychodid genera, still stand. Tonnoir (1940) lists seven genera of PSYCHODIDAE as British, *Pericoma* Walker, *Clytocerus* Eaton, *Telmatoscopus* Eaton, *Psychoda* Latreille, *Trichopsychoda* Tonnoir, *Trichomyia* Haliday and *Sycorax* Haliday. Nothing is known of the larvae of *Clytocerus* and *Trichopsychoda*, whilst that of *Trichomyia* (Keilin and Tate, 1937) is so profoundly modified to a wood-boring life that it differs from *Pericoma* in almost every detail, having no tubular respiratory siphon, no tergal plates, and an antenna consisting of a stout, digitiform process. The larva of *Sycorax* (Bangerter, 1928; Feuerborn, 1933) also differs considerably in having long, four-jointed antennae, a retractable prothorax, and only a single tergal plate to each segment. Of the larvae of the sixteen British species of *Psychoda*, fourteen have been described (Satchell, 1947) and they are much more like those of *Pericoma* than the previous two genera. A number of features have been suggested for separating larvae of the two genera; Walker (1856), Muttkowski (1915) and Malloch (1917) use the form of the siphon, stating that it is long and slender in *Psychoda*, and short in *Pericoma*. The distinction does not apply, however, to *Pericoma fusca*, nor to Johannsen's (1934) Species A, both of which have siphons longer than the majority of *Psychoda* larvae. The presence, in *Pericoma* alone, of preanal and adanal plates has been used as a character by Zavattari (1924) and Johannsen (1934), and, whilst adanal plates are present in both genera, preanal plates do appear to be absent in *Psychoda* larvae, and offer a consistent and convenient method of distinguishing the two genera. Johannsen (1934) uses the difference in the vestiture, contrasting the generally hairy covering of *Psychoda* with the sclerotized thorns of *Pericoma*. There is a real generic difference in this feature, though such species as *Psychoda surcoufi* Tonnoir approach rather closely to the *Pericoma* condition. A character not previously suggested, which appears satisfactory among all the species examined by the writer, is the antenna. In *Psychoda* it consists of a group of sensory processes covered by a domed vesicle shaped like an inverted watch-glass. In *Pericoma* the sensory processes are larger and quite uncovered (fig. 3E).

There appears to be no generic character separating the larvae of *Pericoma* from those of *Telmatoscopus*, but our knowledge of the larvae of this genus is very poor. Of the twenty-three British species, the larvae of two are known; that of *T. ustulatus* Walker (Feuerborn, 1926) is like that of *P. trivialis*, and lives amongst decaying sea grass on the coast, whilst that of *T. decipiens* Eaton (Feuerborn, 1923) has a thick covering of lime and lives in limy springs, like *P. trifasciata*. Three other species of larvae have been described which do not occur in Britain. That of *T. albipunctatus* Willis, a cosmopolitan species, occurs amongst a variety of decaying organic matter, both animal and vegetable, and looks like a typical *Pericoma* larva with well-



FIGS. 21–26.—Dorsal surface of seventh abdominal segment of various species of *Pericoma*, all × 76. (21) *P. fuliginosa*, (22) *P. neglecta*, (23) *P. trivialis*, (24) *P. fusca*, (25) *P. diversa*, (26) *P. calcilega*.

developed dorsal setae (Efflatoun, 1920; Zavattari, 1924; Williams, 1942). *T. similis* Tonnoir (Feuerborn, 1926), with the same habitat as *T. ustulatus*, has a somewhat similar larva with a rather shorter siphon and is a European species. *T. horai* Tonnoir, an Indian species, the larva of which was described by Tonnoir (1933) has a row of six ventral suckers, like a Blepharocerid larva, and lives in torrential streams. When the larvae of more species of this genus have been described, it will probably be found that they have undergone an adaptive radiation quite as extensive as that of *Pericoma* larvae, occupying a number of the very diverse habitats that marginal conditions provide. Separation of the larvae of these two genera can thus only be by specific characters.

Acknowledgments.

It is a pleasure to acknowledge my indebtedness to Mr. Paul Freeman, of the British Museum, both for his checking of my identifications of the *Pericoma* flies and for some assistance with the literature. The material for this paper was collected whilst I was holding an appointment at Nottingham University, and I am indebted to the Research Committee of Senate for a grant towards the travelling expenses involved. Thanks are also due to Dr. E. J. W. Barrington and Professor B. J. Marples for the departmental facilities kindly afforded me.

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CONTENTS

PAGE
KHALIFA, A., B.Sc.(Cairo), Ph.D.(Cantab.). Spermatophore production in Trichoptera and some other insects . . . . . 449–471, 14 figs.
GENERAL INDEX 473–479

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SPERMATOPHORE PRODUCTION IN TRICHOPTERA AND SOME OTHER INSECTS.

By A. Khalifa, B.Sc.(Cairo), Ph.D.(Cantab.).
Department of Entomology, Zoological Laboratory, Cambridge.

Manuscript received 14th April, 1949.
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With 14 Text-figures.

Contents.

PAGE

I. Trichoptera :

Introduction 449
Category A. Forms producing spermatophores . . . 450
The spermatophore-producing organs 450
The female organs concerned with the reception of the spermatophore 452
The structure and fate of spermatophores of different species . 455
Mating and spermatophore formation 457
An aberrant form 459
Category B. Forms delivering free sperm 460

II. Neuroptera :

Sialis lutaria L. (Sialidae) 460

III. Hymenoptera :

Pimpla instigator F. (Ichneumonidae) 461
IV. Discussion 462
V. Summary 468
VI. Acknowledgments 469
VII. References 469

I. Trichoptera.

Introduction.

The Trichoptera have been little studied in respect of the structure of the reproductive system and the method of sperm transference. Cholodkovsky (1913) is the only author to have examined the contents of the *bursa copulatrix* of two species, viz. *Goera pilosa* Fabricius and *Molanna angustata* Curtis. He reported that he found structures which could be regarded as spermatophores, but he showed reluctance to call them genuine spermatophores, as he presumed that they originated partly in the female receptacle, and so recommended the term "spermatodose." He defined a spermatodose as a structure which arises within the female receptaculum and serves for determining the amount of sperm necessary for fertilizing the eggs. The term was also recommended by the same author for similar structures found by Siebold (1845) in the female receptacle of some locustids, and identified at that time as spermatophores. Cummings (1916) accordingly applied the term to sperm sacs found in the female receptacle of *Ibidaecus plataleae* Denny, and *I. flavus* Cummings (Mallophaga) without providing evidence that they arose within the female receptacle during copulation.

As far as Trichoptera are concerned it seems that Cholodkovsky's opinion was based on a casual dissection of these two species of caddis flies without aiming at finding out the identity of these structures. His definition can by no means be applied to the structures found in the female organs of insects examined in this work. When copulation was deliberately interrupted and the insects were examined, it became evident that the sperm sac and another associated protein mass, which were regarded as the components of the spermatophore, were coming from different parts of the male sexual tract. The fluid found in the bursa before copulation, which is presumably secreted by the bursa gland, is a transparent colourless fluid and has the function of digesting the protein mass, rendering it soluble and absorbable.

Cholodkovsky's comment, I believe, is all that can be found in the literature with regard to the existence of spermatophores in Trichoptera. Many other authors, Zander (1901), Stitz (1904), Cholodkovsky (1911), Dodson (1935), and Deoras (1944) have described morphologically the internal and external genitalia of different types of caddis flies. Deoras has unjustifiably created names for certain parts of the genital tract which would give a false idea of their function. He calls a certain part of the male accessory glands which contains large protein globules "epididymis," and describes the female bursa which receives the products of copulation as the "shell gland."

Twelve species of caddis flies were examined, most of which could be brought to copulate under laboratory conditions. Those which have swarming habits, such as *Mystacides nigra* L., were carefully caught during the process of copulation, when they were found sitting on reeds and other plants near the water, brought to the laboratory and examined when required. All caddis flies were offered sugar solution during the time they were kept in the laboratory. Multicopulation has been repeatedly observed in males and females of many species. But the products of a second copulation are much less in quantity than those of the first; the protein mass is much smaller and the sperm sac is reduced in size.

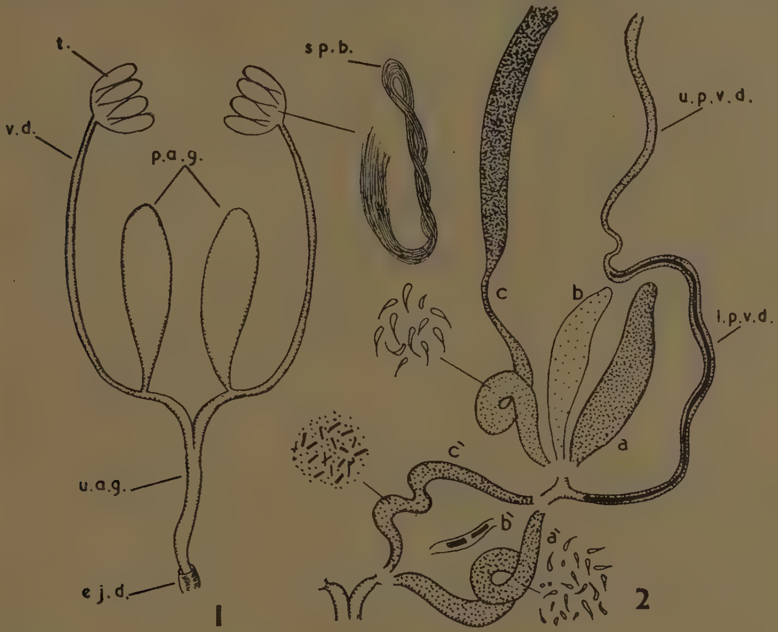
In Trichoptera the external genital organs are all essentially the same, yet genuine spermatophores do occur in certain species while others receive free sperm. This phenomenon shows that there are two types of internal genital organs performing sperm transference in two different ways: the production of spermatophores and the delivery of free sperm. The species dealt with in this work are grouped, therefore, into two categories representing the two kinds of insemination.

Category A. Forms Producing Spermatophores.

This category is represented by the following species:

Sericostoma personatum Spence	SERICOSTOMATIDAE.
Silo nigricornis Pictet	
Molanna angustata Curtis	MOLANNIDAE.
Anabolia nervosa Curtis	LIMNOPHILIDAE.
Halesus radiatus Curtis	
Limnophilus politus McLachlan	

The spermatophore-producing organs.—In order to understand the process of spermatophore formation it is necessary to give a short description of the male sexual tract of this type of caddis flies. The male internal genital organs of all caddis flies are built up on the same morphological basis (fig. 1). In the above-mentioned forms each *vas deferens* (v.d.) is divisible into two main parts separated by a narrow portion. In fig. 2 the upper part, whose length differs from one species to another, is transparent and contains a fine granular secretion which clearly shows Brownian movement. This secretion resembles that which accompanies the sperm in the sperm sac. The lower part contains a milky white secretion whose granules are much bigger and stick together when they come out in water or Ringer solution. This part is very long in forms like *Sericostoma* and *Anabolia* while comparatively short in *Molanna*. The amount of secretion in this part of the *vasa deferentia* corresponds to the size of the sperm sac; the more the secretion the bigger the sac.



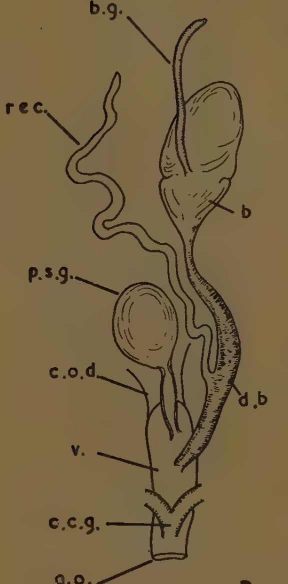
FIGS. 1–2.—(1) The male reproductive system in Trichoptera. ej.d., ejaculatory duct; p.a.g., paired accessory glands; sp.b., sperm bundle; t., testis; u.a.g., unpaired accessory gland; v.d., vas deferens. (2) A diagrammatic representation showing the modification in the male reproductive system in *Sericostoma personatum* (*a* and *a'*), *Molanna angustata* (*b* and *b'*) and *Anabolia nervosa* (*c* and *c'*). l.p.v.d., lower part of *vas deferens;* u.p.v.d., upper part of same.

At the end of the *vasa deferentia* a pair of accessory glands branches off. They greatly differ in length and colour. In *Sericostoma* and *Silo* they are short glands containing a very fine, milky, granular secretion (*a*). In *Molanna* they are of the same length but contain a transparent fluid (*b*). Because of their transparency a few sperm bundles were occasionally observed in them moving up and down as the muscular wall contracts. The *vesiculae seminales* are lacking in all caddis flies examined, and so sperm bundles generally leave the testes only during the time of copulation. In *Anabolia* the paired accessory glands are very long (*c*) and almost fill the body cavity. Each gland can be divided into two parts: the proximal segment, which is short and milky in colour, contains a great number of large protein bodies mostly oval in shape, the distal part is much longer and contains a dark red gelatinous secretion. In *Halesus* and *Limnophilus* the paired accessory glands attain such a length, but are yellowish green in the former and pink in the latter. There is a definite correlation between the amount of secretion found in the paired accessory glands and the size of the female *bursa copulatrix*; the more the secretion the bigger the bursa.

After the point at which each gland branches off, and before the two lateral ducts coalesce there is a special part of the tract which differs in length from one species to another. In *Sericostoma* and *Silo* it is a long coiled duct containing a great number of large oval protein granules (*a*′). In *Molanna* it is very short and contains parts of the same sort of secretion found in the proximal part of the *vas deferens* (*b*′). In *Anabolia* and the other limnophilids it is long and contains a mixture of rod-shaped bodies and fine granules (*c*′). When the two lateral ducts coalesce they form one single tube, the unpaired gland, which goes towards the posterior end where it joins the muscular ejaculatory duct. The unpaired accessory gland secretes in all cases a transparent jelly-like fluid. The ejaculatory duct is highly muscular and goes through the cuticular penis.

The female organs conerned with the reception of the spermatophore.—The female organs (fig. 3) are by far the most characteristic of this category of caddis flies. These organs are built up on a common morphological and physiological basis for holding the sperm sac and making use of its associated protein mass. The genital opening leads to a vagina which is a tubular passage supported from the sides by different sclerites. It receives first the duct of the huge colleterial glands (c.c.g.) and after a short distance the opening of the *ductus bursae* (d.b.). Closely after comes that of the pear-shaped gland (p.s.g.). The *ductus bursae* receives the *bursa copulatrix* (b.) and a side long tubular structure (rec.) with a reservoir at its proximal end. The reservoir is found in forms like *Sericostoma* and *Silo* (fig. 4*a*), but disappears in *Anabolia* and the other limnophilids (fig. 5*a*). This tubular structure is called the "flagellum" by Stitz (1904) and Dodson (1935), but it is shown by Cholodkovsky (1913) that it functions as a *receptaculum seminis*.

The *bursa copulatrix* is the sac which receives the products of copulation. In *Anabolia* and all limnophilids it attains a very large size (fig. 5*a*) and is provided with a cuticular lining which is in the form of sharp teeth in the fundus region (fig. 5*b*). In a virgin female the bursa is a collapsed sac containing a small amount of a colourless transparent secretion; but in a recently copulated female, especially in forms like *Sericostoma*, *Silo* and all limnophilids, it is comparatively large as it is filled with the secretion from the male accessory glands. The walls of the bursa can be greatly stretched so as to hold two or three spermatophores resulting from two or three successive copulations (fig. 6*a*). The bursa of *Halesus* is a very big sac and acquires a disc shape when filled. From the bursa there arises a tubular gland which differs in length from one species to another (fig. 3, b.g.). In *Molanna* (fig. 7, b.g.) it is a very short, bifurcated structure coming out from the top of the bursa, but in *Anabolia* and its closely related species it is a very long tube with many muscular bands along its length and with very big glandular cells (fig. 5*a*, b.g. and fig. 8*a*). In *Sericostoma* and *Silo* the gland is shorter and nearly as long as the bursa itself (fig. 4*a*, b.g.). There is a correlation between the length of the bursa gland and the size of the protein mass accompanying the sperm sac; the bigger the mass the longer the gland.



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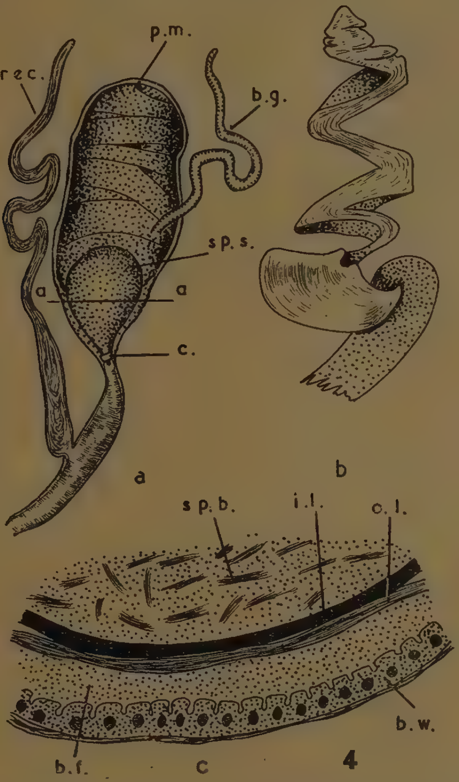

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Figs. 3–4.—(3) A general diagram showing the female organs concerned in the reception of the spermatophore. b., bursa copulatrix; b.g., bursa gland; c.c.g., common duct of the colleterial glands; c.o.d., common oviduct; d.b., ductus bursae; g.o., genital opening; p.s.g., pear-shaped gland; rec., receptaculum seminis; v., vagina. (4) *Sericostoma personatum*: (*a*) Bursa containing a spermatophore; (*b*) the protein mass stretched; (*c*) T.S. through *a–a*. b.g., bursa gland; b.f., bursa fluid; b.w., bursa wall; c., calyx; i.l., inner layer of sperm sac; o.l., outer layer of same; p.m., protein mass; rec., receptaculum seminis; sp.b., sperm bundle; sp.s., sperm sac.

In *Sericostoma*, *Silo* and *Molanna* the spermatophore is deposited as a whole in the bursa copulatrix and the neck of the sperm sac is held in position by a cuticular calyx[1] at the anterior end of the *ductus bursae* (fig. 4*a* and 7*c*.). In *Anabolia* and the other limnophilids the protein mass is deposited in the bursa while the sperm sac is placed in the *ductus bursae* (fig. 5*a*). In these forms the calyx, which is a dark brown conspicuous structure, is to be found along the duct. In *Sericostoma* and *Molanna* it is white and thus is difficult to see except in sections.

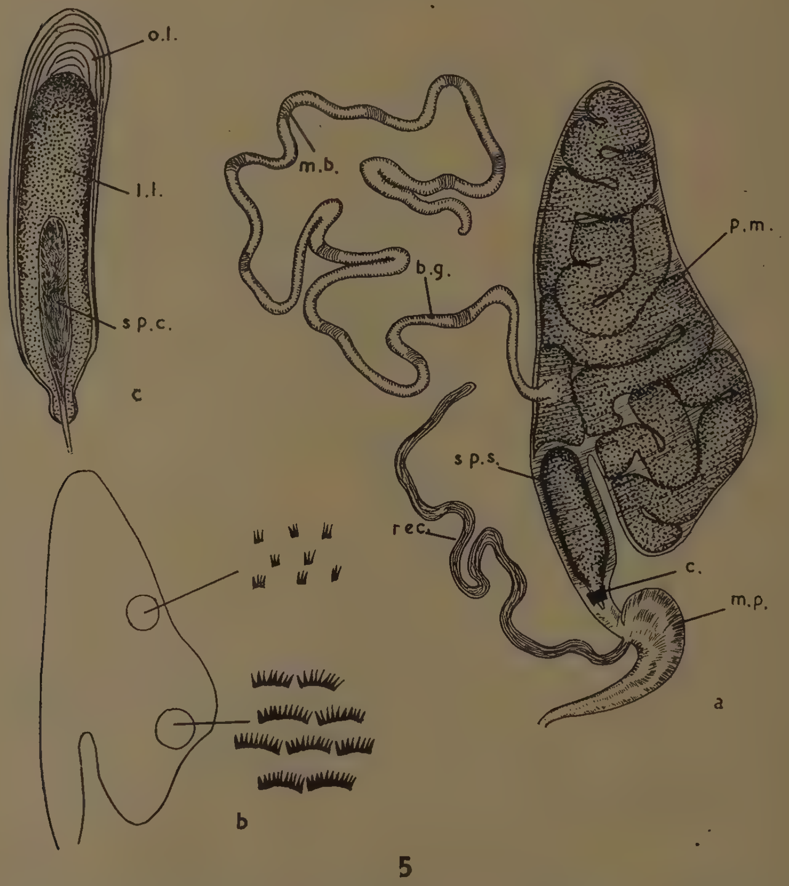

Fig. 5.—*Anabolia nervosa*: (*a*) Bursa containing a spermatophore; (*b*) the lamina dentata; (*c*) the sperm sac. i.l., inner layer; m.b., muscular band; m.p., muscular part of ductus bursae; o.l., outer layer; sp.c., sperm capsule. For further explanation of lettering see fig. 4.

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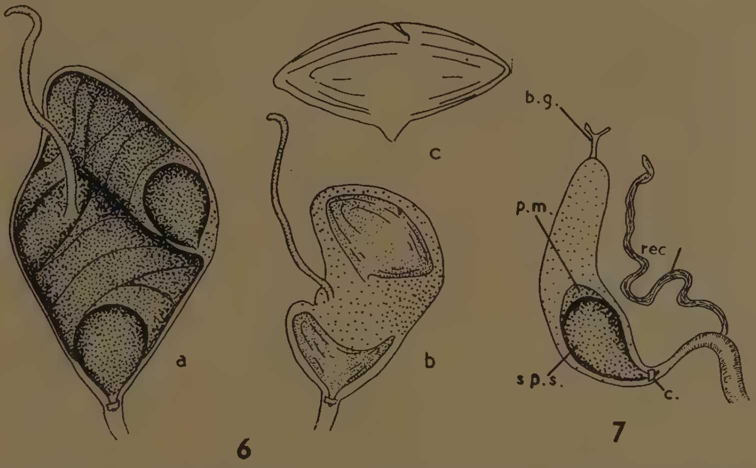
[1] I propose this term for the cuticular ring in the *ductus bursae* of insects belonging to this category.

The pear-shaped gland (fig. 3, p.s.g.) contains a transparent fluid, some crystals of different shapes and air bubbles. In *Anabolia* it contains a great number of rod-shaped bacteria which move actively in Ringer solution. The bacteria appear in great numbers when the adult is 5–7 days old. Similar bacteria were also observed in the pear-shaped gland of *Halesus*. The pear-shaped gland is considered by Stitz (1904) as the *receptaculum seminis*, but according to Cholodkovsky (1913) it is a gland of unknown function. This gland was examined several times during the present work and it was found to contain a small number of motionless sperm only on two occasions in *Sericostoma*. In the " flagellum " the sperm are normally stored and show active movement in Ringer solution ; the gland may be a reservoir of some excretory products.



Figs. 6–7.—(6) *Sericostoma personatum* : (*a*) Bursa containing two intact spermatophores ; (*b*) the protein masses have been digested and absorbed ; (*c*) a collapsed sperm sac. (7) *Molanna angustata*, bursa containing a spermatophore. For explanation of lettering see fig. 4.

The structure and fate of spermatophores of different species.—As has been stated, the spermatophore of this category of caddis flies is composed mainly of two different parts : a coagulated protein mass and a sperm sac. The latter contains no chitin and is mainly protein. In *Sericostoma* the protein mass (fig. 4*a*, p.m.) is a white milky structure weighing about 0·2 mg. and occupies nearly two-thirds of the bursa. The sperm sac is nearly spherical, about 0·9 mm. long and 0·83 mm. wide, and weighs about 0·02 mg. when empty. It has a very short neck carrying a narrow opening at its tip. In sections the sperm sac appears to have an outer lamellated and inner homogeneous layer (fig. 4*c*).

The different parts of the spermatophore undergo important changes in the female bursa. Twelve hours after copulation the protein mass becomes softer and loses its coiled form ; twelve hours later it is nearly dissolved.

Two days after copulation all traces of the protein mass disappear and the empty sperm sac and the bursa collapse (fig. 6*b*). The bursa of a wild female may have one or two collapsed sperm sacs; it may have a recently deposited spermatophore with an old collapsed sperm sac at the top, or two intact spermatophores the result of two successive matings, one soon after the other (fig. 6*a*). *Silo* agrees with *Sericostoma* in all details save that the sperm sac is a little smaller, as it measures 0·66 mm. in length and 0·21 mm. in width.

In *Molanna* the protein mass is much smaller (fig. 7, p.m.) and the sperm sac is about 0·36 mm. in length and 0·26 mm. wide. Multicopulation seemed to be of rare occurrence since never more than one spermatophore was found in the bursa. The bursa gland is here very much reduced in size; there is little need for secretion as the protein mass has been reduced to a very small size.

In *Anabolia* the protein mass has a very long coiled tubular form, a dark red colour and occupies the whole cavity of the bursa (fig. 5*a*, p.m.); its weight soon after copulation amounts to 3·28 mg. The sperm sac (fig. 5*c*) is a milky white rod-shaped body about 1 mm. in length and 0·25 mm. in width. Its wall consists of two layers which are relatively thin at the sides but very thick at the top. The sperm sac is deposited in the *ductus bursae* and its neck is held by the calyx in such a way that its opening comes to lie near the opening of the spermatheca.

Twelve hours after copulation the protein mass loses its original consistency and acquires that of thick dough. It changes in colour from dark red to transparent white, starting at the bottom of the bursa (fig. 8*b*). The change in colour proceeds and the white mass is gradually absorbed, and in the course of 9–10 days the mass completely disappears (fig. 8*f*). It has been digested and absorbed. The bursa then collapses and its walls assume a brownish colour. In the *ductus bursae* the sperm sac undergoes similar changes. By the time the protein mass disappears the walls of the sperm sac become very thin and the thick top part almost degenerates (fig. 8*f*); it loses its original toughness and becomes very soft. The cells of the bursa gland also degenerate (fig. 8*f*).

When a female copulates for a second time the old sperm sac is forced to take another position inside the bursa, where it is found squeezed and collapsed. Up to three sperm sacs were found in such condition. It is doubtful, however, that a female can digest and absorb more than one protein mass during the short span of her imaginal life. There is no conspicuous connection between the absorption of the protein mass and the ripening of eggs in the ovaries. Ripe eggs appear in the ovaries 4–5 days after emergence whether copulation takes place or not. It is likely, therefore, that this big mass of protein is used in nutrition as these insects do not take much food during their imaginal life.

In *Halesus* the protein mass is of a yellowish green colour and occupies the whole cavity of the disc-shaped bursa. The sperm sac is similar in shape to that of *Anabolia* and about 1·3 mm. long and 0·33 mm. wide. The fate of the spermatophore is similar to that of *Anabolia*; the protein mass is digested and absorbed in a similar way and the sperm sac collapses and partly degenerates.

In *Limnophilus* the protein mass is pink and is deposited in the bursa. The sperm sac is about 1·16 mm. in length and 0·33 mm. wide and the fate of the spermatophore is identical.

Mating and spermatophore formation.—Wesenberg-Lund's (1943) description of the mating of *Mystacides nigra* L. is typical for all caddis flies examined. Copulation was performed in a glass tube and the process observed under the binocular microscope. The male proceeds sideways to the female underneath her wings, holds her thorax with his front legs, and bends his abdomen to insert the protruded penis into her genital aperture. When this is secured the male turns 180° and the two insects assume an end-to-end position. They remain as such for a varying length of time ranging from 3–8 hours. But

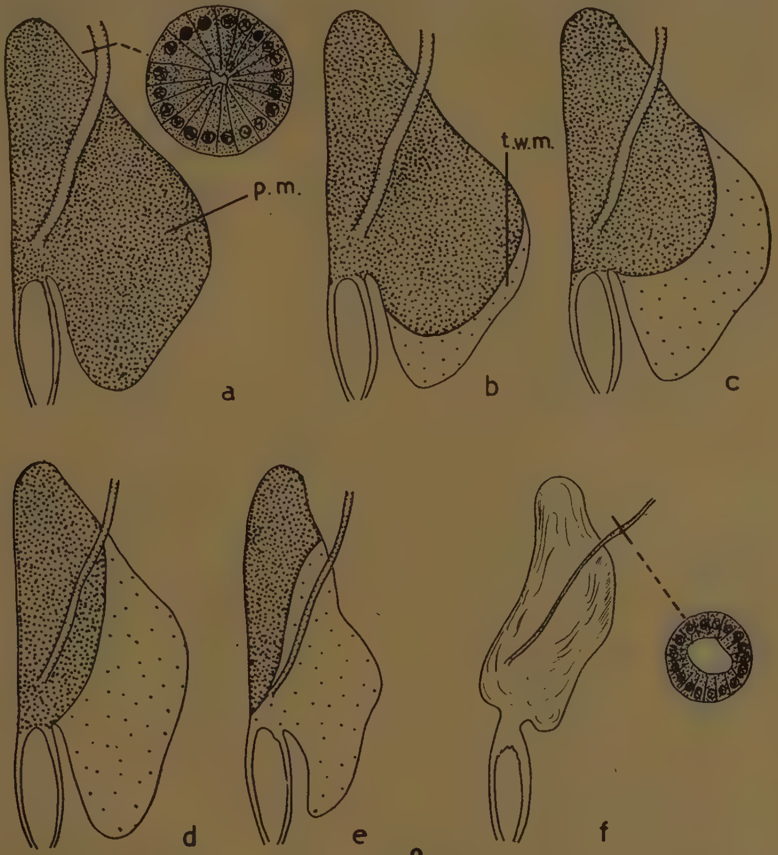


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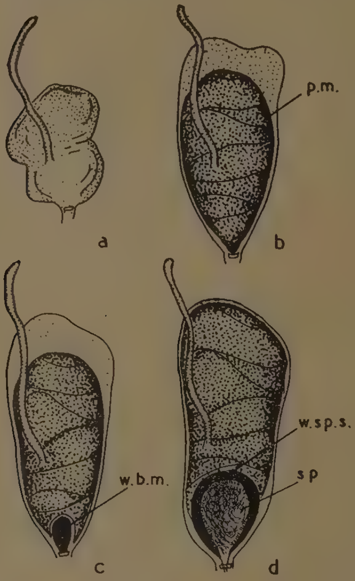
FIG. 8.—*Anabolia nervosa.* The fate of the spermatophore. (*a*) Bursa full of the dark red protein mass. A section through the bursa gland is also shown; (*b*) 12 hours after copulation. The change in colour appears at the bottom of the bursa; (*c*) 24 hours; (*d*) 48 hours; (*e*) 6 days; (*f*) 9 days, the bursa is empty and collapsed and the sperm sac is degenerated. A section through the gland is also shown. p.m., protein mass; t.w.m., transparent white mass.

building the spermatophore inside the female bursa does not take this length of time; a couple remains *in copula* long after the products of copulation are delivered.

During copulation the contents of the unpaired gland is poured into the bursa followed by the contents of the paired accessory glands. The two secretions mingle in the bursa and a thick mass of protein, thicker than either of the original secretions, is formed (fig. 9*b*). The term "spermatophylax" is proposed for this protein mass since it shows homology with the spermatophylax of the tettigonid spermatophore. They originate from the male accessory glands and in a way perform the same function, i.e. food for the female.



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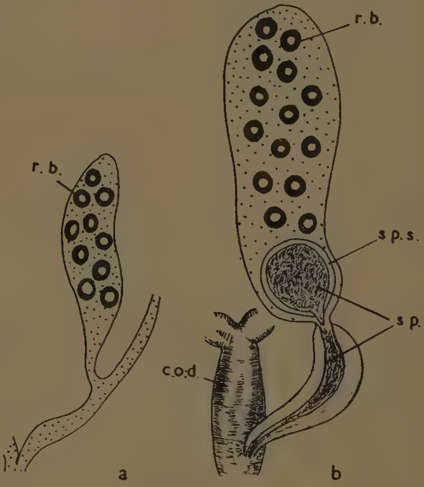

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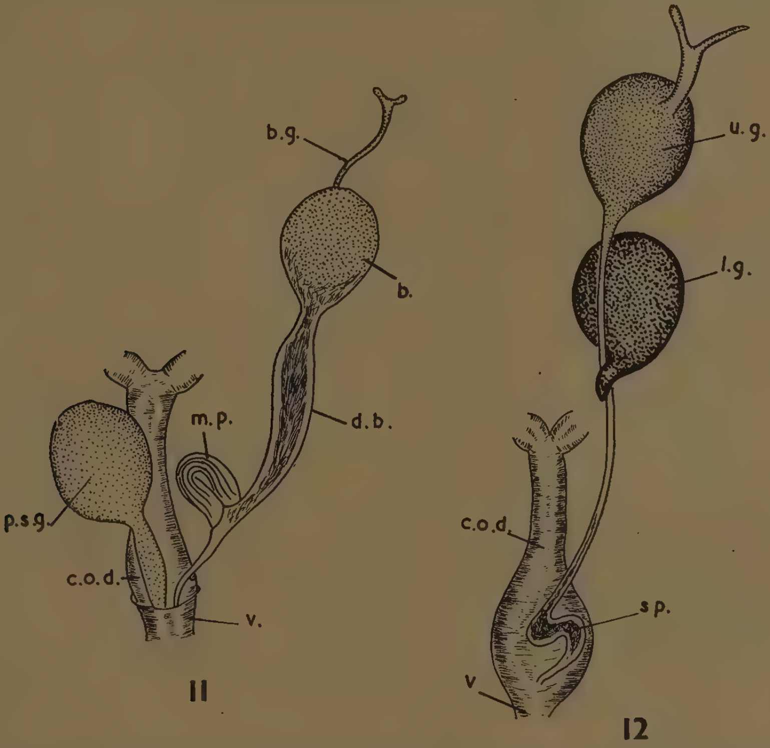
Figs. 9–10.—(9) *Sericostoma personatum*. The formation of the spermatophore: (*a*) An empty bursa; (*b*) the deposition of the protein mass; (*c*) the deposition of the secretion of the lower parts of the vasa deferentia; (*d*) the delivery of sperm. p.m., protein mass; sp., sperm; w.b.m., white blocked mass; w.sp.s., wall of the sperm sac. (10) *Lype phaeopa*: (*a*) One of the paired accessory glands; (*b*) the bursa copulatrix. c.o.d., common oviduct; r.b., round body; sp., sperm; sp.s., sperm sac.

The next step in the process of spermatophore formation is the ejection of the contents of the lower parts of the *vasa deferentia*. This secretion forms in the bursa, or in the *ductus bursae* near the calyx, a white silvery blocked mass (fig. 9*c*). Soon, however, by an unknown mechanism it acquires a cavity and grows gradually in size as the sperm and the fine granular secretion of the upper parts of the *vasa deferentia* are pushed in (fig. 9*d*). The sperm sac is more or less spherical in those species where it is deposited in the bursa, viz. *Sericostoma*, *Silo* and *Molanna*, while elongated in *Anabolia* and the other limnophilids where it is moulded in the *ductus bursae*. The position of the calyx along the *ductus bursae* determines the place and eventually the form of the sperm sac.

An aberrant form, belonging to this category but not fitting the foregoing description, is the very small caddis fly, *Lype phaeopa* Stephens (Psychomyidae).



Figs. 11–12.—(11) *Cyrnus trimaculatus*, female genital organs. b., bursa copulatrix; b.g., bursa gland; c.o.d., common oviduct; d.b., ductus bursae; m.p., muscular part; p.s.g., pear-shaped gland; v., vagina. (12) *Tinodes waeneri*, female genital organs. c.o.d., common oviduct; l.g., lower gland; sp., sperm; u.g., upper gland; v., vagina.

The *vasa deferentia* are short, containing a transparent secretion and the paired accessory glands contain a number of round bodies with transparent centres and opaque outlines suspended in a transparent fluid (fig. 10*a*). They gave fat and protein negative reactions, they did not dissolve in dilute acids but dissolve quite readily in a dilute solution of KOH. Of the female organs only the bursa copulatrix is represented (fig. 10*b*).

The sperm sac is spherical, about 0·18 mm. long and 0·13 mm. wide. It has a short neck lying in the anterior end of the ductus bursae and a thin transparent wall. A protein mass is lacking but a number of the round bodies found in the male accessory glands are transferred to the bursa during copulation. A spermatheca is lacking and so most of the sperm are kept in the sperm sac, but some migrate to the *ductus bursae*.

Category B. Forms Delivering Free Sperm.

This category is represented by the following species:

Mystacides nigra L.	LEPTOCERIDAE.
M. azurea L.	
Polycentropus flavomaculatus Pictet	POLYCENTROPIDAE.
Cyrnus trimaculatus Curtis	
Tinodes waeneri L.	PSYCHOMYIDAE.

The result of copulation in this group has been ascertained by examining the insects soon after copulation.

The female organs in *Mystacides* spp. are morphologically the same as those of the first category. There is a bursa with a bursa gland coming off at the top, a spermatheca and a pear-shaped gland. The result of copulation is the delivery of free sperm in the bursa, a part of which migrates to the spermatheca. In *Polycentropus* and *Cyrnus* there are a pear-shaped gland and a bursa, but there is no spermatheca (fig. 11). The result of copulation is the delivery of free sperm in the bursa which functions in this case as a receptaculum. In *Tinodes* the female organs are built up on a different scheme. The vagina (fig. 12) gives rise to a very fine duct which is attached to two spherical glands at the anterior end. In a virgin female the most anterior gland is filled with a milky granular secretion, but the posterior one contains a greenish mass of thick consistency. After copulation these contents are almost exhausted and the milky granular secretion of the anterior gland is used and disappears first. The function they perform is unknown, but it may be presumed that they serve as nourishment for the sperm. The result of copulation is the deposition of free sperm in the posterior part of the duct (fig. 12, sp.).

II. NEUROPTERA.

Sialis lutaria L. (SIALIDAE).

The spermatophore of *Sialis* (fig. 13) is of a vase shape and consists of two essential parts: a body and a neck. The body is about 0·6 mm. long and 1 mm. wide in the widest part. It contains two distinct cavities containing the sperm and the associated granular substance. Each cavity is surrounded by a thick transparent inner layer (i.l.) and contains a white milky mass. The two chambers are enclosed in another outer thinner membrane which at the basal part of the neck takes an irregular form. The neck is about 1·5 mm. in length and 0·4 mm. wide at its basal end. It is formed by the continuation of the inner walls of the two chambers. Through the neck go two narrow tubes commencing at the top of the two chambers and ending blindly at the distal end of the neck. The two tubes are also full of a white milky fluid similar to that which occupies the sperm cavities.

The spermatophore is built inside the male accessory glands and ejected just at the moment of copulation. When ejected it is a soft structure and can be forced to take any shape; it hardens, however, as soon as it comes into contact with the air and becomes very brittle. During copulation the neck of the spermatophore is inserted into the opening of the female *bursa copulatrix*; the body remains outside for a while. Later the spermatophore slides into the female genital opening and bits of the outer covering remain outside and eventually fall off. Inside the bursa the spermatophore is broken into pieces by the contraction of the very strong muscular walls of the bursa and by the help of the sharp cuticular spines which line the cavity of the bursa in certain areas. The sperm, consequently, are set free in the bursa and migrate into the spermathecae, one of which is found on each side of the *bursa copulatrix*.

After a time which differs greatly from one individual to another, the female, twisting her body to bring her mouthparts close to the genital opening pulls out the remaining parts of the spermatophore and chews them up. In *Osmylus chrysops* David (1936) stated that the spermatophore is provided with a big spermatophylax to which the female is attracted and which she eats while the sperm migrate to the spermathecae and so escape destruction. The spermatophylax, which is built up of protein, remains outside the female genital opening and may stay there for a varying length of time ranging from 10 minutes to 2 days.

Withycombe (1924) was of the opinion that spermatophores seem to be a characteristic feature of Neuroptera, although they are not always easily seen. He stated that they do not occur in CONIOPTERYGIDAE, perhaps, because of the presence of a true penis.

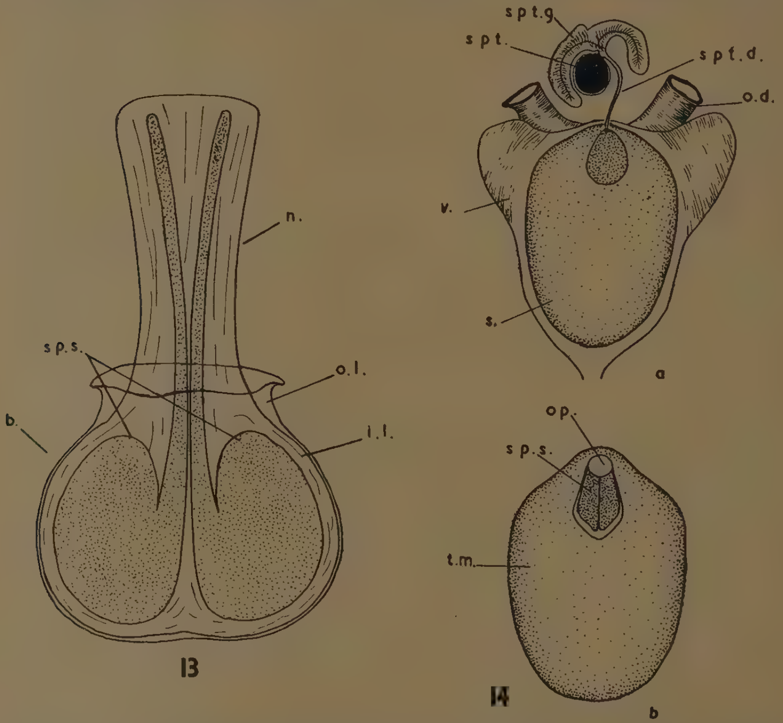
III. HYMENOPTERA.

Pimpla instigator F. (ICHNEUMONIDAE).

The insects were sexually mature and ready to copulate soon after emergence. When a recently-copulated female was dissected the vagina was found to contain a spermatophore. It occupied most of the cavity of the vagina, which took a more or less round shape (fig. 14*a*). The opening of the spermatophore was in direct connection with the opening of the spermathecal duct and so firmly fixed in it that it was very difficult to dislodge. Twelve hours after copulation, however, the opening of the spermatophore was released from that of the spermathecal duct so that the spermatophore could easily be removed from the vagina.

The spermatophore (fig. 14*b*) is a transparent egg-shaped body about 0·66 mm. in length and 0·61 mm. wide. There is a small milky portion at the anterior end containing a double sperm sac with a common opening which has a conspicuous rim. The latter fits in the opening of the spermathecal duct which is lined at its proximal end with a thick layer of cuticle. The body of the spermatophore is held in the vagina, presumably, by the sharp cuticular teeth lining it. Each sperm sac is triangular in shape and has a double wall made of a milky secretion. The two sacs are surrounded by the big transparent mass which forms the body of the spermatophore. Soon after copulation the sperm start to migrate into the spermatheca and within

2 or 3 hours the sperm sacs are empty. The empty spermatophore, which retains its normal shape, is kept in the vagina for 16–20 hours, after which it is ejected through the copulatory opening ; the walls of the vagina, eventually, collapse and no sign of the spermatophore remains. Multiple copulation seems not to occur as never more than one spermatophore was found in the vagina. The ageing of virgin females had a great effect on their readiness to mate. Females of 5–7 days of age never had a tendency to copulate although the accompanying males made several attempts. They continued to lay unfertilized eggs which gave male offspring.



FIGS. 13–14.—(13) *Sialis lutaria*, spermatophore. b., body of spermatophore ; i.l., inner layer ; n., neck of spermatophore ; o.l., outer layer ; sp.s., sperm sacs. (14) *Pimpla instigator* : (*a*) Female genital organs shortly after copulation ; (*b*) spermatophore. o.d., oviduct ; op., opening of the spermatophore ; s., spermatophore in vagina ; sp.s., sperm sacs ; spt., spermatheca ; spt.d., spermathecal duct ; spt.g., spermathecal gland ; t.m., transparent mass ; v., vagina.

IV. DISCUSSION.

Authors who have dealt with the biology and sexual behaviour of insects, or even with the morphology and function of the copulatory apparatus, very often leave one in doubt as to whether copulation is by means of a spermatophore or by delivering free sperm in the female organs. This is not surprising because spermatophores are not easy to detect and are modified and destroyed after transfer to the female. Unless the observer watches the process of copulation and examines the female soon after, it is difficult to tell whether free sperm or a spermatophore has been delivered. The problem is made much more difficult by the odd distribution of spermatophores among insects. It is hardly possible to assert that they occur in all insects of a certain order or even in all species of a single family. In most orders it has been found that closely related species whose male copulatory apparatus are morphologicaly the same, differ in the method of sperm transference, some delivering free sperm and others spermatophores.

The problem of spermatophore production in insects will be discussed here in a wider sense, taking the allied groups, viz. Onychophora, Crustacea, Myriapoda and Arachnida into consideration. This is to show that spermatophores are sporadically distributed among the arthropods, and to bring to light some facts which might help in understanding how spermatophore-formation has evolved.

In Onychophora a true copulation does not take place. It has been known for a long time that the male *Peripatus* deposits small white oval spermatophores indiscriminately on any part of the body of the female. Manton (1938) cleared up the problem in *Peripatopsis*, showing that sperm penetrate the walls of the spermatophore, pass through an area of the cuticle which has become perforated under the spermatophore, and pass along the vascular channels to the ovary. *Peripatopsis* thus resembles the leech *Clepsine* in that the sperm migrate through the body wall in order to fertilize the eggs. Among insects, *Cimex* shows a more or less similar behaviour ; the sperm are ejected into a specialized area of the intersegmental membrane between the 5th and 6th abdominal sternites (Ribaga's organ), penetrate a matrix of cells (Berlese's organ) and find their way to the spermathecae through the body cavity.

In Crustacea the use of spermatophores as a means of insemination is carried out in two big groups : Copepoda and Malacostraca (Euphausiacea, Decapoda), while free sperm are transferred in Branchiopoda (Cladocera), Ostracoda, Cirripedia and some other groups of Malacostraca (Isopoda, Amphipoda). In *Crangon vulgaris* (Decapoda) Lloyd and Yonge (1947) showed that, owing to the absence of copulatory organs, spermatophores are applied to the ventral side of the female usually adjacent to the genital opening. In *Homarus*, *Nephrops* and *Cambarus*, Yonge (1945) showed that spermatophores were forced into the spermatheca by the help of some modified abdominal appendages. In *Palaemonetes vulgaris* (Decapoda), Burkenroad (1947) showed that spermatophores adhere to the body wall near the female genital opening and eventually the sperm are liberated into the water, where external fertilization takes place. These authors, together with Ray Lankester (1909), Mouchet (1931), Spalding (1942), Cronin (1947) and King (1948), agree in that the *vasa deferentia* of most decapods are responsible for secreting the material of and building up spermatophores.

In *Daphnia*, Snodgrass (1936) and Wesenberg-Lund (1939) stated that the fertilization of the winter eggs is carried out in the brood pouch by the delivery of free sperm. In *Cypris acuminata* the latter author showed that copulation occurs with the direct transference of sperm into the female genital opening.

In Cirripedia it is well known that the bisexual reproduction in *Lepas* is carried out by the penis protruding and depositing a mass of sperm on either side of the mantle cavity of a neighbouring individual in the vicinity of the opening of the oviduct. Lastly, in *Asellus* and *Gammarus*, Maercks (1930) and Heinze (1932) showed that free sperm were found to be delivered during copulation.

In Myriapoda, which are closely related to Insecta, it is known that most Chilopoda form spermatophores. The males deposit spermatophores in places frequently visited by females, which, in some still unknown way, take them up. The male *Geophilus* spins a web and deposits a spermatophore in the middle; the female comes to the web to be fertilized.

In Arachnida it has been stated by Kew (1912) that the male chelonethid (Pseudoscorpione), after a preliminary courtship, deposits a spermatophore on the ground. This consists of a rod with a globule containing the sperm at one end. The male directs the female towards the spermatophore which thrusts into her genital opening as she passes over it. In the argasid tick, *Ornithodorus moubata*, Robinson (1942) showed that a peculiar spermatophore is transferred over to the female during copulation. In HYDRACHNIDAE it has been shown by Viets (1936) and Motas (1928) that in *Acercus ornatus* and *Brachypoda versicolar* respectively the transference of sperm takes place by the formation of spermatophores. The former author, however, showed that in other aquatic mites, e.g. *Piona longicornis*, only a bundle of sperm is transferred. Lundblad (1929) has indicated that among the aquatic mites *Arrhenurus globator* also delivers free sperm. External fertilization takes place in the Xiphosura: the male of *Limulus polyphemus* spreads the sperm over the eggs. In Scorpionidea, Phalangida, and Pedipalpida a direct contact of the genital apertures and presumably the transference of free sperm take place. In the other groups of Arachnida the use of the palpal organs is a common occurrence during mating.

This brief survey of the Arthropoda other than insects shows in how many different ways the crucial and practically difficult problem of sperm transference has been solved, and that spermatophores have been developed again and again, in a phylogenetically disconnected manner, as one solution of the problem. The distribution of spermatophores within each of these arthropod groups needs further investigation.

Among the insects, no verified observations have yet been made of the exact manner of insemination of the female by the male in the Apterygota. These insects have rarely been seen during coitus. *Thermobia domestica* (Thysanura) has been observed *in copula* by Spencer (1930) and his observation was confirmed by Sweetman (1934). They recorded that the male performs a dance in front of the female during which a spermatophore is dropped. It is picked up by the female and inserted into her genital opening. Another record on the curious mating habits of the SMINTHURIDAE (Collembola) is given by Lie-Pettersen (1899) and commented on by Snodgrass (1936). The male was seen to emit a drop of spermatic fluid; using his front legs he smeared the drop on his mouth-parts and inserted the latter into the female genital opening.

The emission of free sperm or of spermatophores by the primitive insects, Chilopoda and Pseudoscorpione, and the deposition of spermatophores on the body of a female *Peripatus* support the idea that the original ancestor of insects must have had some such mode of insemination ; in other words, it did not have the method of delivering free sperm directly into the female organs characteristic of the higher insects. Tiegs (1940) envisaged some ancient aquatic *Peripatus*-like ancestor of tracheate arthropods shedding its reproductive cells into the water. When such an animal took to life on land, he suggested, internal fertilization would have to occur. While the development of internal fertilization by spermatophore, or direct internal delivery would have advantages, e.g. in economizing sperm, to aquatic animals and such devices are found among them in many forms, nevertheless external fertilization is quite easy in water whereas for the terrestrial animal it is almost impossible. Considering the diversity and crudity of the internal fertilization methods employed by the primitive arthropods, it seems likely that they did not come from an aquatic ancestor which had already developed a method of internal fertilization, but had to face the problem anew. Thus the crude device for achieving internal fertilization in *Peripatus* by attachment of spermatophores to the body wall of the female probably reflects its primitive adaptation to a terrestrial environment. It seems safe to conclude, therefore, that the habit of spermatophore-formation among insects is a primitive character.

In Orthoptera there is far more agreement with regard to the method of sperm transference than in any other insect order. Spermatophores are common to the five big groups, viz. Acridoidea, Blattoidea, Mantoidea, Phasmatoidea and Tettigonioidea and have undergone modification in structure according to the evident evolution of the copulatory apparatus. A general study of the male internal and external reproductive system in Orthoptera leads one to separate these main groups into three main categories on the basis of the mode of spermatophore production and delivery.

In group 1, which may be considered the most primitive, a spermatophore is developed long before copulation, kept in what is called a dorsal sac or a spermatophore mould until the male comes across a female and tries to deliver it. When copulation takes place the spermatophore remains hanging outside the female opening. The *Gryllus domesticus* spermatophore is very elaborate and provided with a very efficient mechanism whereby the sperm are passed from it to the spermatheca. This group includes the Tettigonioidea, comprising principally TETTIGONIIDAE and GRYLLIDAE. The spermatophores in this group fall into two main divisions : some with one main sperm sac, e.g. those of *Gryllus*, *Nemobius*, *Liogryllus*, *Oecanthus*, *Gryllotalpa*, and very likely all representatives of the family GRYLLIDAE ; the second division comprises spermatophores with two or more sperm sacs, e.g. those of the family TETTIGONIIDAE. This type of spermatophore is almost always surrounded by a huge albuminous covering which is termed the " spermatophylax."

Group 2 is represented by the two big superfamilies, Blattoidea and Mantoidea. Here spermatophores are developed only during copulation, which extends generally over a longer time, and when delivered to the females the spermatophores are held by certain external sclerites concealed completely in Blattoidea and partly in Mantoidea by the subgenital plates. In this way the process of sperm delivery is more secure and so less primitive.

Group 3 is represented by Acridoidea. Here the spermatophores are of a very simple tubular structure, perhaps on account of the development of an intromittent organ, and inserted as a whole into the female spermathecal duct during copulation. It represents the simplest and most advanced mode of insemination among the Orthoptera. It does not involve the production of a spermatophylax which protects the sperm sacs against being eaten by the female nor any of those sexual behaviour patterns performed after the delivery of a spermatophore in GRYLLIDAE.

With regard to Phasmatoidea it has been stated by Snodgrass (1937) that the exact use of their copulatory apparatus and the occurrence of spermatophores have never been recorded. He seems to have overlooked a reference by Chopard (1934), who recorded the occurrence of a spermatophore in *Phyllium bioculatum* of the family PHASMIDAE. He states that it is a spherical structure about 2 mm. in diameter and has a cylindrical tube which is inserted into the female genital opening. It resembles in appearance the spermatophores of *Nemobius* and *Gryllus*, and remains outside the female genital opening for a long time after copulation. There is no mention of whether it is formed before or during the process of copulation. A study of the copulatory apparatus of a phasmid, however, would suggest that it would develop during the process since there is no dorsal sac. Phasmatoidea, therefore, would be included in the 2nd group.

Of the Grylloblattoidea there is no record of spermatophore production. It has been suggested by Snodgrass (1937) that the type of spermatheca found in *Grylloblatta* suggests the occurrence of spermatophores. This statement in fact means little since it is unknown which type of spermatheca would require a spermatophore. The matter is, therefore, still open for further investigation. Of Embioptera and Isoptera records are also lacking.

A higher stage of sperm transference would be a corresponding specialization of the female internal sexual organs which could take in the spermatophore and keep it temporarily or permanently. In Acridoidea this stage is accomplished. The *Sialis* spermatophore is kept in the bursa copulatrix for a short time and in Lepidoptera and Trichoptera it is kept, but in a modified condition, till the female dies. In most cases the spermatophore then serves as a provisional sac holding the sperm until they find their way to the spermatheca. In one case only, that is in the caddis fly, *Lype phaeopa* (p. 459), the spermatophore is kept in use during the entire life of the female. My preliminary examination[2] of Mallophaga suggests that it is more than likely, indeed practically certain, that the "sperm sacs" found by Kramer (1869) and Cummings (1916) in the spermathecae of some lice are genuine spermatophores. This is, therefore, another case of depositing spermatophores in the spermatheca where they are kept permanently in use. Each sperm sac is kept in use until the next one resulting from a second copulation is deposited.

After the stage in which specialized parts of the female genital organs have become adapted to accommodate the spermatophores there has been a tendency to lose them and to deliver free sperm directly into the female organs. In Hymenoptera the first record of spermatophore production is that of Flanders (1939) for *Calliephialtes extensor*. In *Macrocentrus ancylivorus* the same author (1945) found that sperm transference from the male to the female occurred by means of spermatophores. On the other hand it has long been known that no spermatophore exists in the honey-bee and in the present work it has also been found that *Athalia lineolata* (TENTHREDINIDAE) delivers free sperm during copulation.

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[2] Lice preparations were kindly supplied by Miss T. Clay.

In Coleoptera, Muir (1919) realized that there are several types of internal and external male sexual organs and pointed out that it was reasonable to expect that they would function in different ways. He drew attention to the probability of finding spermatophores in those species which possess an internal sac (a bladder-like structure which evaginates and acts as an intromittent organ). He stated that when this sac was provided with a long tubular flagellum-like structure it was highly probable that no spermatophore would be found. If, however, no specialized sac (one without a flagellum) was present a spermatophore was most likely to be formed. This deduction was brought about by the morphological study of the copulatory apparatus of many species but seems to find support in the work of Harnisch (1915) and Rittershaus (1927). Harnisch studied the method of sperm transference in some chrysomelid beetles, and found in *Lina populi* a sac equipped with a long flagellum which he called a "praepenis." The sac was found to occupy the vagina while the flagellum goes through the spermathecal duct. So a direct connection between the two sexes is established during copulation whereby free sperm are transmitted. Rittershaus, on the other hand, found highly developed sacs with no flagella in three scarabid beetles, viz. *Phyllopertha horticola*, *Anomala aenea* and *Amphimallus solstitialis* where copulation was carried out by spermatophores. But in spite of this, Muir's statement, as it appears, does not give a satisfactory answer to the question of spermatophore production in this group, since not only forms with flagella deliver free sperm but also certain forms that have internal sacs without flagella, e.g. *Telephorus fulva*. In addition, there is the large group of Coleoptera in which the male copulatory apparatus has an undifferentiated internal sac and both methods of sperm delivery are found ; *Tenebrio molitor* and *Dytiscus marginalis* are examples—a spermatophore is found only in the latter. In Coleoptera it is, in fact, difficult to give any general scheme for spermatophore production. Cros (1924) found and described the spermatophores of some tenebrionid and scarabid beetles and ascertained that in each family there are two groups : one forming spermatophores and the other delivering free sperm, a phenomenon which was found applicable to CANTHARIDAE, CHRYSOMELIDAE and CURCULIONIDAE. Of the CANTHARIDAE, *Cantharis nigricans* var. *discoideus* forms a spermatophore while *Telephorus fulva* delivers free sperm. Of the CHRYSOMELIDAE, *Haltica lythri* produces a spermatophore while it does not exist in *Donacia semicuprea*. Finally, *Apion pomonae* (CURCULIONIDAE) was found by Stein (1847) to possess a spermatophore while *Phyllobius urticae*, which belongs to the same family, was found during the present work to deliver free sperm. In all beetles examined spermatophores are kept temporarily in the vagina and ejected when empty ; there is no record of their being used in nutrition.

The sperm transference of a few Hemiptera has been studied. Besides the well-known case of *Cimex*, Ludwig (1925) found in *Lygaeus equestris* an extraordinarily long penis which reaches the opening of the spermatheca during copulation. Such a direct connection between the penis and the female spermatheca was found to occur in another lygaeid, *Onchopeltis fasciatus*, and in the aquatic bugs, *Nepa*, *Notonecta* and *Corixa*. In these forms it has been found that free sperm are delivered directly into the female organs. In

Rhodnius prolixus and *Triatoma infestans* (Reduviidae), although there is a very large aedeagus which is evaginated and fills the vagina during copulation, there is no direct connection between it and the spermathecae. The sperm mass is deposited in the very large vagina and brought into touch with the opening of the common oviduct (the uterus of Galliard, 1935) by enclosing it in a big spermatophore which occupies the vagina till a certain amount of sperm finds its way to the spermathecae. The empty collapsed spermatophore together with the excess of sperm are ejected by the female shortly after copulation (Khalifa, *in press*).

The ability of the sexual organs to deliver free sperm seems to be dependent on structural and physiological adaptations which are closely linked together. The structural adaptation is apparent in those forms of Coleoptera and Hemiptera where a direct connection between the male copulatory apparatus and the female spermatheca is established. In this case the spermatheca is physiologically adapted to preserve free sperm accompanied only by secretion from the male accessory glands. In other cases no such connection is accomplished and yet free sperm are deposited in the vagina, from where they are directed towards the spermatheca. The physiological adaptation is here performed by factors governing the sperm vitality of the orientation of which very little is known.

In Diptera it seems that spermatophores have been lost completely, since no records of them could be found. Five species have been examined: *Tipula lateralis* (Tipulidae), *Ptychoptera contaminata* (Ptychopteridae), *Sphaerophoria picta* (Syrphidae) *Scatophaga stercorarium* (Cordyluridae) and *Calliphora erythrocephala* (Calliphoridae), and in all the sperm were found to be ejected directly into the spermathecae. This advanced method of insemination can be found with varying frequency in most other groups of insects. In this connection Tillyard (1918) may be quoted: "There are, in any given order, many diverse groups. Some of these will exhibit very high specializations in one or more directions; others will show unexpected archaisms. . . ."

The relationship of families in many orders has not yet been indicated with any clearness. In those orders where spermatophores are known to occur in some groups but not in others it may be of some help in deciding their relationship if the character of spermatophore-production be considered. From a practical point of view the spermatophores which, as in certain Orthoptera, remain outside the female genital organs and so can be collected in quantity, would offer the physiologist incomparable material for the study of sperm and the problem of fertilization in insects and other arthropods.

V. Summary.

In Trichoptera there are two types of sperm delivery, namely, the production of spermatophores and the transference of free sperm into the female organs.

The most important feature of the female reproductive organs of spermatophore-producing species is the presence of a cuticular calyx along the *ductus bursae* which holds the neck of the sperm sac. The *bursa copulatrix* is provided in most cases with a well-developed gland which is most likely responsible for

digesting the "spermatophylax." This is a protein mass secreted by the male accessory glands and delivered to the female during copulation.

In the other category of caddis flies the bursa copulatrix is used as a *receptaculum seminis*. It has been found that *Lype phaeopa* and *Tinodes waeneri* which belong to the family Psychomyidae differ in the manner of sperm transference; one forms spermatophore while the other delivers free sperm. Such a difference may exist in other closely related species.

The spermatophore of *Sialis lutaria* (Neuroptera) and *Pimpla instigator* (Hymenoptera) are described.

The discussion may be summarized as follows: (1) Spermatophores are sporadically distributed among most groups of arthropods and their production is considered a primitive character. (2) Spermatophores occur more frequently among the primitive and generalized groups of insects and tend to disappear among the more advanced ones. (3) The loss of spermatophores has occurred independently and with varying frequency from group to group, from family to family, and even from species to species. All Orthoptera have spermatophores and at the opposite extreme all Diptera are without them.

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INDEX

New names are marked with an asterisk.

*_abdicans, Philonthus_, 305, 313
Abraxas, 50
abyssinus, Philonthus, 305, 315
acholica, Pseudacraea, 73
ACRIDIDAE, British, structure and maturation of ovaries, 233–247
aemulus, Philonthus, 361, 362
aenea, Anomala, 467
aequale, Dasus, 258
aesyca, Squamulotilla, 226
aethiopicus, Philonthus, 350
aethiops, Philonthus, 306, 317
affinis, Bombus, 23
affinis, Philonthus, 305, 306
Agagles, 47
Agapetus, 277
agrorum, Bombus, 3, 9–45
alba, Deilemera, 48
albicorne, Odontocerum, 277, 286, 287, 289
albimaculata, Amauris, 73
albipennis, Psychoda, 414
albipunctatus, Telmatoscopus, 445
albomarginatus, Chorthippus, 233–240
algeriana, Oedipoda, 363
algeriana, Thalpomena, 364
algeriana, Thalpomena algeriana, 365, 366
Alphitobius, 258–260, 262–264, 266, 268
Alphitophagus, 267
alternata, Psychoda, 418
amans, Timulla amans, 228
amartano, Timulla philippinensis, 211
Amauris, 73
americanorum, Bombus, 33, 34
Amphimallus, 467
amplificata, Nyctemera, 64
amplipennis, Distretus, 258
Anabolia, 450, 452–460
ancylivorus, Macrocentrus, 466
angustata, Molanna, 449, 450
annulata, Nyctemera, 48, 61, 64
annulipes, Chelonus, 156
Anomala, 467
Anomalipus, 258, 267
anthracinum, Nyctemera, 54, 63
Apatidea, 278
Apion, 467
*_Arctata_ (_Nyctemera_), 50
arcuata, Nyctemera, 49, 63
*_armeniacus, Pseudoceles_, 376, 381
*_arpatchai, Pseudoceles_, 376, 384
Asida, 258, 260, 267
assimile, Nyctemera tripunctaria, 53, 61, 62
assimilis, Nyctemera, 49, 53, 54, 61, 63, 64
Atasca, 47
aterrimus, Leptocerus, 279, 281
Athalia, 467
*_athalia, Smicromyrme_, 219–222
atralba, Nyctemera, 47, 53, 64
auricula, Apatidea, 278
auriculata, Pericoma, 412
aurora, Cophotylus, 388, 389
aurora, Wernerella, 363
Austroicetes, 157
avicularia, Pericoma, 412
azurea, Mystacides, 279, 460
azureipennis, Thalpomena, 364, 365, 372

BAETIDAE from India and S.E. Asia, 161–177
Baëtis, 162–163
basicornis, Philonthus, 305, 309
*_basipennis, Philonthus_, 351
bataviana, Timulla (_Trogaspidia_), 217–218
baulus, Nyctemera baulus, 50–52, 55, 63
Bematistes, 72, 73, 74
bicolor, Chorthippus, 233–247
bicolor, Cloëon, 173
bicolor, Philonthus, 305, 306
bicolor, Pseudacraea, 100, 114
bicolor, Triaenodes, 276, 280
bicoloripennis, Philonthus, 318, 324
*_bedentiformis, Philonthus_, 362
bifasciatus, Alphitophagus, 267
bimaculatum, Procloëon, 176
bioculatum, Phyllium, 466
*_biparamerosus, Philonthus_, 358
bisignatus, Philonthus, 345
Blaesoxipha, 242, 243, 246
blandula, Pericoma, 412, 421, 422, 438, 439
Blaps, 258, 260, 262, 265–267
Blapstinus, 258, 260, 266, 267
boiei, Zophosis, 258, 264
boisduvalii, Pseudacraea, 72, 84
bombi, Sphaerularia, 3
Bombus, 1–45
borealis, Bombus, 16
Brachycentrus, 276
Brachycoma, 3, 37
burgeoni, Philonthus, 353
buruana, Nyctemera baulus, 51, 63

cadaverina, Phaleria, 267
*_caedator, Philonthus_, 331, 337
caffer, Philonthus, 330, 333
cafra, Nyctemera, 47
calcilega, Pericoma, 411, 412, 419
Calliephialtes, 466
Callimorpha, 47
Calliphora, 468
*_campestre, Centroptilum_, 172
canescens, Pericoma, 411, 412, 418, 435
Cantharis, 467
carbonarius, Psammodes, 267
carpenteri, Philonthus, 305, 309

carpenteri, Pseudacraea poggei, 73
cassiope, Odontomutilla, 228
castaneum, Tribolium, 258–263, 268–269
celebensis, Timulla, 228
Centroptilum, 172
Ceriagrion, 136, 137
cervicornis, Philonthus, 361, 362
Chaetopteryx, 276
chapmani, Philonthus, 354
Chelonus, 156
chiopterus, Culicoides, 180
chloropterus, Philonthus, 305
Chorthippus, 233–247
chrysippus, Danaus, 73
Cimex, 467
cinctus, Philonthus, 318, 328
circumcinctus, Philonthus, 345
*_clambus, Philonthus_, 318, 325
clarki, Pseudacraea clarki, 73
clathrata, Neuronia, 283, 288
clathrata, Nyctemera clathrata, 66
Cloëon, 161, 173
Clytocerus, 444
*_Coenagriocnemis_, 137, 140
*_Coenargiocnemis_, 137, 143
coeruleipennis, Thalpomena, 364, 373
coerulescens, Thalpomena, 365, 366, 374
cognata, Pericoma, 411, 412, 418, 423–425
*_Coleta_ (_Nyctemera_), 53
combustus, Philonthus, 330, 333
compta, Pericoma, 412
confusa, Nyctemera, 49, 53, 64
confusum, Tribolium, 255, 258–269
congoensis, Philonthus, 331, 335
Coniontis, 267
conradti, Philonthus, 356
conradti, Pseudacraea, 103, 114
consanguinea, Pseudacraea, 91, 109
consobrina, Nyctemera, 63
*_constricticeps, Philonthus_, 347
contaminata, Ptychoptera, 468
Cophotylus, 363, 366; key to spp. 388
Corixa, 467
cornutus, Gnathocerus, 258, 259, 262, 266, 268
*_crameri, Nyctemera crameri_, 53, 63
*_cribricephalicus, Philonthus_, 318, 323
*_Crinita_, 363, 366, 390–392
cruciata, Austroicetes, 157
Crypticus, 258
Culicoides, seasonal and daily incidence in Scotland, 179–190
*_cumaeus, Philonthus_, 330, 333
cupreonitens, Philonthus, 330, 332
*_curiosus, Philonthus_, 296, 298
Cyrnus, 460

Danaus, 73
dardanus, Papilio, 71, 72, 74
Dasus, 258, 262, 264, 265, 267
decemlineata, Leptinotarsa, 157
decipiens, Telmatoscopus, 445
decora, Smicromyrme, 222–225
Deilemera, 47, 48, 50
deludens, Pseudacraea deludens, 73
*_demavendi, Pseudoceles_, 376, 382
densecaudatus, Philonthus, 345
dentifascia, Nyctemera, 49, 50, 63
depressus, Dasus, 264
deserta, Squamulotilla, 225
*_deserta, Thalpomena_, 365, 366, 373
destructor, Tribolium, 258–266, 269
devia, Brachycoma, 3, 35
Diaclina, 268
diaperinus, Alphitobius, 258–260, 262–264, 268
*_diaphana, Nyctemera_, 64
dilutior, Philonthus, 300
dilutipes, Philonthus, 331, 339
dimidiaticornis, Philonthus, 305, 309
*_dipsicus, Baëtis_, 163
discoideus, Catharis nigricans, 467
distincta, Nyctemera distincta, 54, 57, 63
Distretus, 258, 267
diversa, Pericoma, 412, 419, 421, 435
dollmani, Philonthus, 362
dolomena, Pseudacraea, 73
domestica, Thermobia, 464
domesticus, Gryllus, 465
Donacia, 467
dorsalis, Rhyacophila, 284
Dytiscus, 467

*_elbursi, Pseudoceles_, 377
echeria, Amauris, 73
echerioides, Pseudacraea deludens, 73
egina, Acraea, 73
egina, Pseudacraea clarki, 73
*_elbursi, Pseudoceles_, 376, 384
Eleodes, 258–263, 265, 267
elgonensis, Philonthus, 305, 315
elongata, Bematistes, 73
elutella, Ephestia, larvae of, during diapause, 147–159
Embaphion, 261, 263, 265, 267
Emyon, 267
Enoicyla, 277
epaeoïdes, Pseudacraea, 99, 113
Ephestia, 147–159
epigea, Pseudacraea, 92, 110
equestris, Lygaeus, 467
erato, Timulla, key to males of related spp., 199
erythrocephala, Calliphora, 468
eurytus, Pseudacraea, 71–133; development of knowledge of forms of, 74; immature stages, 76; synonymy, 77–84; male genital armature, 84; forms of, 88–105; distribution of forms, 105–116; mimetic relationships, 116–127.
evergista, Deilemera, 47, 57
exilis, Palorus, 268
exquisita, Pericoma, 412, 419, 422, 436, 439
extensor, Calliephialtes, 466
extricata, Pericoma, 412

fallax, Pericoma, 412, 419, 422, 438, 439
familiaris, Odontomutilla familiaris, 226
famula, Nyctemera, 47
fasciatus, Onchopeltis, 467
fascipennis, Culicoides, 188
femoralis, Pedinus, 258, 260, 262
fickei, Pseudacraea, 103, 114

fimbriolatus, Philonthus, 352
flavicauda, Philonthus, 305, 306
flavicornis, Limnophilus, 276, 281, 284
flavomaculatus, Polycentropus, 460
flavus, Ibidaecus, 449
**fluitans, Baëtis*, 166
Formica, 408
**fraxinatus, Philonthus*, 331, 341
fuliginosa, Pericoma (Ulomyia), 412, 418, 421, 422, 442, 444
fulva, Telephorus, 467
fulvaria, Pseudacraea, 93, 110
furva, Oecetis, 278
fusca, Formica, 408
fusca, Pericoma, 411, 412, 421, 441, 444
fuscipes, Agapetus, 277

Gabrius, 292, 294, 362
gages, Platyscelis, 258, 260
geniculatus, Trachynotus, 258, 267
gerardi, Philonthus, 353
gigantea, Eleodes, 258
Gilpinia, 157
glabrum, Ceriagrion, 136, 137
Gnathocerus, 258, 259, 262, 266, 268
Goëra, 277, 449
Gomphocerus, 233–238
**gongulus, Philonthus*, 356
gottbergi, Pseudacraea gottbergi, 73
gracilis, Pericoma, 412
grandis, Philonthus, 361, 362
**grisea, Pseudacraea*, 100, 113
grisescens, Culicoides, 184, 187, 188
griseus, Trachynotus, 267
Gryllotalpa, 465, 466
Gryllus, 465, 466

haematocephala, Odontomutilla, 226
haematodes, Philonthus, 305, 308
Halesus, 450, 452–460
halophila, Blaps, 258, 260, 262, 265, 266
halophilus, Culicoides, 187
Haltica, 467
**hargreavesi, Philonthus*, 354
Harungana, 74
harveyi, Procloëon, 176
heliophilus, Culicoides, 181–190
**hemixantha, Pseudacraea*, 95, 111
herklotsii, Nyctemera, 51, 54, 56, 63
herpa, Odontomutilla, 227
hesperia, Nyctemera, 47
hibernica, Pericoma, 412
**hirsutus, Philonthus*, 305, 312
hirtipes, Crinita, 391
hirtipes, Thalpomena, 363
hirtum, Lepidostoma, 281, 284
hispilaris, Eleodes, 259, 262, 265
hobleyi, Pseudacraea, 94, 110
hoffmannseggi, Dasus, 258, 262, 267
Homala, 267
horticola, Phyllopertha, 467
hortorum, Bombus, 20–26
hospes, Philonthus, 330, 331
hostilia, Pseudacraea, 72, 73, 84
Humble-bees, biology of, 1–45
humilis, Bombus, 21, 25
hyalina, Nyctemera, 64

Hydropsyche, 277
Hydroptila, 280, 281, 287
Hypophloeus, 266

Ibidaecus, 449
imitator, Pseudacraea, 104, 114
impunctatus, Culicoides, 181–190
impuncticollis, Philonthus, 296
incerta, Formica pallidefulva schaufussi, 408
inconstans, Nyctemera, 49, 63
infestans, Triatoma, 468
**infumata, Pseudacraea*, 96, 111
infuscata, Nyctemera infuscata, 65
**inopinum, Pseudocloëon*, 171
instar, Nyctemera, 55
instigator, Pimpla, 461–462, 469; spermatophore production in, 461
insulare, Coenargiocnemis, 135, 137, 143, 146
**intermedia, Thalpomena algeriana*, 365, 368
**iranicus, Cophotylus*, 388, 390
**iridescens, Philonthus*, 318, 326
Ischnura, 137, 138, 140
itambusa, Timulla philippinensis, 210

**jacksoni, Pseudacraea*, 100, 113
jacobaeae, Callimorpha, 47
javana, Nyctemera arctata, 63
jeanneli, Philonthus, 305, 311
**julia, Cloëon*, 176

**kangeana, Timulla philippinensis*, 211, 214
**kashituensis, Philonthus*, 318, 324
kellyi, Smicromyrme, 218
kondekum, Deilemera, 55
kondekum, Leptosoma, 61
kondekum, Nyctemera, 49, 53, 64
kraatzi, Philonthus, 347
kraepelini, Pseudocloëon, 171
kristenseni, Philonthus, 305, 308
kühniella, Ephestia, 156, 157
künowoides, Pseudacraea, 96, 111

lachesis, Pseudacraea, 97, 113
lacticinia, Nyctemera, 47, 48, 53, 63
laevigatus, Alphitobius, 258
laevinodis, Myrmica, 393–409
lampropterus, Philonthus, 300
lapidarius, Bombus, 17, 20, 21, 24, 25, 32, 33
lateralis, Tipula, 468
Latheticus, 258, 266, 268
laticornis, Philonthus, 362
latistriga, Nyctemera latistriga, 55, 56, 63
latreillellus, Bombus, 4
ledereri, Pseudoceles, 375, 385
ledereri, Thalpomena, 363
leucostigma, Nyctemera, 49, 56, 63
Lepidostoma, 281, 284, 287
Leptinotarsa, 157
Leptocerus, 279, 281, 287
Leptosoma, 47
lethifera, Blaps, 258, 260, 266
**limbata, Nyctemera*, 65
Limnophilus, 276, 281, 284, 287, 450, 452–460
Lina, 467

lineatus, Stenobothrus, 233–247
lineolata, Athalia, 467
Liogryllus, 465
*_lissonurus, Philonthus_, 331, 341
Locusta, 236
Loxostege, 156
lucanicornis, Philonthus, 361, 362
Lucilia, 157
lucorum, Bombus, 2, 12, 14, 16, 17, 21, 24, 25, 32, 33, 37
*_lugens, Nyctemera_, 65
lutaria, Sialis, spermatophore production in, 460–461, 469
lutosa, Asida, 258, 260
Lygaeus, 467
Lype, 459, 466, 469
lythri, Haltica, 467

Macrocentrus, 466
*_macrogyna, Myrmica rubra_, 397–408
maculata, Nyctemera, 50, 63
maculata, Nyctemera maculata, 49, 57, 63
maculatus, Myrmeleotettix, 233–247
maculipennis, Philonthus, 348
madagascariensis, Harungana, 74
madens, Tribolium, 268
maderae, Oedipoda, 363
madianus, Philonthus, 304
major, Formica rufa rufo-pratensis, 408
*_malayana, Methoca_, 195–196
malayana, Timulla philippinensis, 211, 212
manifesta, Odontomutilla, 227
manyemae, Philonthus, 331, 344
*_marescens, Philonthus_, 331, 342
marginalis, Dytiscus, 467
marginalis, Nyctemera, 49
marginipennis, Philonthus, 318, 328
maritimus, Philonthus, 331
*_maroccana, Thalpomena algeriana_, 365, 369
*_marshalli, Philonthus_, 331, 335
mauriciana, Platycnemis, 137, 145
*_meges, Philonthus_, 330, 332
melaneura, Nyctemera, 52
melas, Nyctemera, 52
methneri, Philonthus, 305, 308
Methoca, 193–198; key to Malayan spp., 194
*_mickeli, Timulla (Trogaspidia)_, 199, 201–204
*_microgyna, Myrmica rubra_, 397–408
Micropterna, 276, 281
migratoria, Locusta, 236
mimo-ras, Pseudacraea, 98, 112
minor, Formica rufa rufo-pratensis, 408
minutus, Philonthus, 345
mlanjensis, Pseudacraea, 104, 114
mocquerysi, Philonthus, 347
Molanna, 449, 450
molitor, Tenebrio, 258, 259, 262–264, 266, 267, 467
mongendensis, Philonthus, 299
*_montana, Thalpomena algeriana_, 365, 368
monticola, Gabrius, 362
morio, Philonthus, 331, 333
motoensis, Philonthus, 317
mundipicta, Nyctemera, 51, 63
muricatum, Embaphion, 261, 263, 265
mutua, Pericoma, 412
Myrmeleotettix, 233–247
Myrmica, 393–409
Mystacides, 278, 279, 450, 460

natalensis, Philonthus, 305, 306, 313
neglecta, Pericoma, 411, 412, 418, 419, 421, 430–432
Nemobius, 465, 466
Nepa, 467
nerina, Nyctemera, 47
nervosa, Anabolia, 450
neumanni, Pseudacraea gottbergi, 73
Neuronia, 283, 288
niavius, Amauris, 73
nigra, Mystacides, 278, 450, 460
nigriceps, Philonthus, 353
nigricornis, Silo, 450
nigripes, Crinita, 391
nigrovenosa, Nyctemera, 52
nigrovenosa, Nyctemera coleta, 48, 52
*_nimboides, Philonthus_, 306, 315
nitidiventris, Formica pallidefulva, 408
Notonecta, 467
noviespunctata, Nyctemera, 49, 63
nubecula, Nyctemera, 49, 56
nubecula, Nyctemera trita, 63
nubeculosus, Culicoides, 188
nubila, Pericoma, 411, 412, 418, 419, 422
Nyctemera, spp. from Java, 47–64; spp. from Malaya, 64–66

obscura, Pseudacraea, 99, 113
obscurus, Pseudoceles, 376, 385
obscurus, Tenebrio, 258–260, 262, 264, 268
obsoletus, Culicoides, 180–189
occulta, Hydroptila, 280, 281, 287
ochripennis, Philonthus, 330, 332
ocypoides, Philonthus, 361, 362
Odontocerum, 277, 286, 287, 289
Odontomutilla, 226–228
Oecanthus, 465
Oecetis, 278
Oedipoda, 363
oedipodioides, Pseudoceles, 376, 380
Omocestus, 233–247
Onchopeltis, 467
Opatrinus, 267
Opatrum, 258, 260, 262, 264–267
opisthoxantha, Pseudacraea, 95, 111
*_orcinus, Philonthus_, 353
orina, Acraea, 73
oryzae, Latheticus, 258, 268
oryzae, Timulla amans, 229
ovada, Nyctemera latistriga, 56, 63

paederomimus, Philonthus, 317, 321
pagenstecheri, Nyctemera, 51, 52
*_palaestinus, Pseudoceles_, 376, 380
pallens, Nyctemera, 49, 56, 63
pallidicornis, Culicoides, 181–190
*_palmyrae, Baëtis_, 163, 164
*_paloeana, Timulla philippinensis_, 211, 215
Palorus, 249–273
palustris, Pericoma, 412

Papilio, 71, 72
parallelus, Chorthippus, 233–247
parciventris, Philonthus, 318
parvicornis, Philonthus, 318, 328
Pedinus, 258, 260, 262, 267
**penthesilea, Methoca*, 196–198
peregrinus, Philonthus, 345
perenna, Acraea, 73
Pericoma, early stages of British spp., 411–447; key to larvae, 418; key to pupae, 421
**peripateticus, Philonthus*, 300, 303
persa, Pseudoceles, 376, 377
persa, Thalpomena, 363
personatum, Sericostoma, 276, 277, 450
petulca, Nyctemera, 53, 61
phaeopa, Lype, 459, 466, 469
Phaleria, 267
philippinensis, Timulla philippinensis, 211, 212
philippinensis, Timulla, keys to related subspp., 210, 211
**Philonthoblerius*, 300
Philonthus, 291–362
Philopotamus, 277
**phoculus, Philonthus*, 305, 309
Phryganea, 284, 286
Phyllium, 466
Phyllobius, 467
Phyllopertha, 467
picatus, Secusio, 51
pilosa, Goëra, 277, 449
pilularia, Pericoma, 412
Pimelia, 258
Pimpla, 461–462, 469
Pitasila, 47
plataleae, Ibidaecus, 449
Platycnemis, 137, 145
Platyscelis, 258, 260, 267
plebeius, Anomalipus, 258
poggei, Bematistes, 73
poggei, Pseudacraea poggei, 73
poggeoides, Pseudacraea, 97, 112
Polistes, 22
politus, Limnophilus, 450
pollux, Philonthus, 362
Polycentropus, 460
polytoma, Gilpinia, 157
pomonae, Apion, 467
**pondo, Pseudacraea*, 104, 114
popiya, Nyctemera, 54
popiya, Nyctemera assimilis, 63
popiya, Nyctemera distincta, 63
popiya, Nyctemera popiya, 57
**popovi, Pseudoceles*, 377, 381
populi, Lina, 467
**praetor, Philonthus*, 317, 319
pratorum, Bombus, 17, 24, 25, 32
prolixus, Rhodnius, 157, 468
Psammodes, 258, 267
pseudabyssinus, Philonthus, 305, 315
Pseudacraea, 71–133; generic synonymy, 77; mimicry in, 73
Pseudagrion, 136, 138
pseudexquisita, Pericoma, 412, 421, 422, 439
Pseudoceles, 363, 366; key to spp., 375, 385
Pseudocloëon, 171
Psithyrus, 3
Psychoda, 412, 414, 415, 418, 444, 445
Ptychoptera, 468
pulchra, Pericoma, 411, 412, 419, 421, 425
pulicaris, Culicoides, 180–189
punctum, Pseudagrion, 135, 136, 138, 146
pusilla, Enoicyla, 277
pusillus, Dasus, 258, 265

quadriguttatum, Nyctemera, 55, 63
quisquiliarius, Philonthus, 331
quisquilius, Crypticus, 258

radiatus, Halesus, 450
**rapaciosus, Philonthus*, 350
ratezeburgi, Palorus, biology of, 249–273
**Raucalius*, 304
reinecki, Philonthus, 299
**rhodesiae, Philonthus*, 317, 319
**rhodesianus, Philonthus*, 348
Rhodnius, 157, 468
rhombicus, Limnophilus, 276
Rhyacophila, 277–278, 280, 284, 286
robusticornis, Philonthus, 318, 328
rogersi, Pseudacraea, 102, 114
rubra, Myrmica, 393–409
rubrocapitata, Odontomutilla, 227
**rubrovittatus, Philonthus*, 317, 320
ruderarius, Bombus, 21
rudipennis, Philonthus, 318, 326
rufa, Formica, 408
rufa, Formica rufa, 408
rufescens, Philonthus, 318, 322
rufipes, 135, 137, 142, 146
rufotincta, Diaclina (Alphitobius), 268
rufus, Gomphocerus, 233–238
rufus, Philonthus, 362
ruginodis, Myrmica, 393
ruginodo-laevinodis, Myrmica laevinodis, 393–409
**rugulipennis, Philonthus*, 300, 301
ruhama, Pseudacraea, 90, 109
**rungsi, Thalpomena*, 365, 366, 374
ruwenzorica, Pseudacraea, 101, 114

sabulosum, Opatrum, 258, 260, 262, 265
sanguineus, Philonthus, 347
scalarium, Nyctemera, 49, 50
scalarium, Nyctemera arctata, 49, 63
Scatophaga, 468
sceva, Timulla (Trogaspidia), 199, 205–208
schoutedeni, Philonthus, 299, 300
scotti, Philonthus, 305, 308
scrobicularis, Psammodes, 258
Secusio, 51
**selene, Timulla (Trogaspidia)*, 199, 200–201
semicuprea, Donacia, 467
senegalensis, Ischnura, 137, 138, 146
**sepilibilis, Philonthus*, 331, 339
**septimum, Cloëon*, 174
sequax, Micropterna, 276, 281
sequens, Philonthus, 330, 333
seriatipennis, Philonthus, 300
sericata, Lucilia, 157
Sericostoma, 276, 277, 450, 452–460
serraticornis, Philonthus, 362

sexmaculata, Nyctemera, 63
Sialis, 460–461, 469
*siccum, Cloëon, 174
Silo, 450, 452–460
similis, Psammodes, 258
similis, Telmatoscopus, 418
simulator, Pseudacraea, 93, 110
simulatrix, Nyctemera, 63
singapora, Timulla philippinensis, 211, 212
*sinuatus, Philonthus, 331, 341
skeati, Timulla philippinensis, 212
*smaragdinus, Philonthus, 348
Smicromyrme, 218
*solitarius, Baëtis, 170
solstitialis, Amphimallus, 467
somaliensis, Philonthus, 318
*sondaica, Timulla (Trogaspidia), 199, 208–209
Sphaerularia, 3
Sphingonotus, 363
splendens, Cophotylus, 388, 389
splendens, Thalpomena, 363
*stavelioides, Pseudacraea, 91, 109
steindachneri, Cophotylus, 388
Stenobothrus, 233–247
stephani, Timulla (Trogaspidia), 199, 204–205
stercorarium, Scatophaga, 468
sticticalis, Loxostege, 156, 157
striata, Pseudacraea, 91, 109
subdepressus, Palorus, 258
subglobosa, Pimelia, 258
subnubilus, Brachycentrus, 276
subsiriatus, Blapstinus, 258, 260, 266
subtilicornis, Philonthus, 362
subveleta, Nyctemera, 66
sulcipennis, Eleodes, 262
sumatrensis, Nyctemera, 64
*sumbana, Timulla (Trogaspidia) philippinensis, 212, 216
sunda, Timulla philippinensis, 211, 213
surcoufi, Psychoda, 445
suturalis, Eleodes, 258, 260–263, 265
Sycorax, 444
sylvarum, Bombus, 21, 25

*tamulus, Philonthus, 358
tandanlensis, Philonthus, 305
*tari, Pseudoceles, 376, 382
Telephorus, 467
Telmatoscopus, 418, 444, 445
Tenebrio, 258–260, 262–264, 266–268, 467
TENEBRIONIDAE, comparative survey of life histories, 258–266 ; natural habitats and feeding habits, 266–268
tenuifascia, Nyctemera tenuifascia, 60, 63
*tenuissimus, Philonthus, 331, 344
terra, Pseudacraea, 99, 113
terrestris, Bombus, 17, 21, 22, 24–26, 32, 33
Thalpomena, 363–391 ; key to spp., 364
thearini, Pseudacraea, 92, 110
Thermobia, 464
*thurbonis, Baëtis, 168
thymele, Odontomutilla, 227
*tigroides, Baëtis, 167
Timulla, 198–218, 228–229
Timulla (Trogaspidia) philippinensis, key to subspecies of, 209–212
Tinodes, 460, 469
Tipula, 468
tirikensis, Pseudacraea, 96, 111
Trachynotus, 258, 267
Triaenodes, 276, 280
Triatoma, 468
Tribolium, 266–269
Trichomyia, 444
Trichopsychoda, 444
Trichoptera, British, pupae of, 275–289 ; spermatophore production in, 449–471
trifasciata, Pericoma, 411, 412, 419, 421, 428, 445
*trilobatus, Philonthus, 331, 335
trimaculatus, Cyrnus, 460
trimeni, Pseudacraea boisduvali, 73
tripunctaria, Nyctemera, 47, 49, 53, 61, 62, 66
tripunctaria, Nyctemera tripunctaria, 60, 61, 63
triseriatus, Philonthus, 300
triste, Opatrum, 258, 262, 264, 265, 266
tristichus, Philonthus, 299
trita, Nyctemera, 56
trita, Nyctemera trita, 62, 64
trivialis, Pericoma, 412, 414, 418, 419, 422-423, 444, 445
Tryphaeromera, 47
turbidus Philonthus, 354
*turcicus, Pseudoceles, 375, 385
*turneri, Philonthus, 344

uelensis, Philonthus, 317, 321
Ulus, 267
*unguicularis, Philonthus, 318, 323
urania, Odontomutilla, 228
urticae, Phyllobius, 467
ustulatus, Telmatoscopus, 418, 445
ustus, Philonthus, 330
*uvarovi, Pseudoceles, 375, 383

varia, Phryganea, 284, 286
velans, Nyctemera, 66
ventralis, Philonthus, 331
victoris, Pseudacraea, 101, 114
villosa, Chaetopteryx, 276
*vinsoni, Ischnura, 137, 140, 146
violaceus, Pseudoceles, 376, 383
viridipennis, Thalpomena, 364, 365, 369, 372
viridis, Cloëon, 174
viridulus, Omocestus, 233-247
vittiger, Philonthus, 317
volvulus, Philonthus, 318, 321

waeneri, Tinodes, 460, 469
williamsi, Timulla philippinensis, 211

youbdonis, Pseudacraea, 92, 109

*zanzeguri, Pseudoceles, 376, 381
zetes, Acraea, 73
Zonosoma, 47
Zophosis, 258, 264, 267
Zygoptera, of Mauritius, 135-146

ERRATA.

P. 78, line 25, *for* " punctus " *read* " punctis."

P. 95, lines 12–15, rewrite as follows : " The model is *Bematistes macarista rileyi* le Doux, and the mimic is perhaps one of the best among all the forms of *eurytus*. The form of *macarista* having the anterior portion of the bar of the hind wing yellow instead of white was shown to be *M. macarista* Sharpe by le Doux (1937)."

P. 101, the date of description of *victoris* should be 1929.

P. 101, lines 7–8 from bottom, *for* "*albostriata* Lathy " *read* " *dolabella* Hall."

P. 118, second paragraph, *for* " Van Someren " *read* " van Someren."

P. 128, line 6, *for* " R. van Someren " *read* " V. G. L. van Someren."